Long-term study (1974–1998) of seasonal changes in the phytoplankton in Lake Geneva: a multi-table approach

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The monitoring of Lake Geneva began after one decade of eutrophication and has provided a uniform set of phytoplankton data. This study aimed to define the mean annual pattern of the seasonal successions of phytoplankton species, and to determine whether inter-annual distortions in this seasonal structure occur. We analysed the 25 annual patterns using the STATIS multi-table method. The phytoplankton successions in the first part of the year fitted well with the pattern predicted by the Plankton Ecology Group (PEG) model. But the temporal evolution in the summer phytoplankton community differed from the PEG model, and was subject to between-years differences. We identified three homogeneous periods for the annual patterns: 1974–1985, 1986–1991 (except 1988) and 1992–1996 (including 1988). During the first period, phytoplankton succession followed the reference annual pattern, the typical autumnal community was missing during the second period, and this autumn community developed earlier during the third period. This study reflects the good ability of the phytoplankton community of Lake Geneva to resist both inter-annual fluctuations and brutal shifts in the annual functioning of the system. We believe these shifts resulted from a gradual change in environmental parameters, including the deepening of the phosphorus-depleted layer and a change in its timing as a result of the long-term meteorological changes.

INTRODUCTION

Hutchinson showed that there are several characteristic patterns of seasonal changes in phytoplankton assemblages (Hutchinson, 1967). It is now widely recognized that succession patterns vary little from year to year and are usually similar in lakes, having analogous climatic conditions, morphometric characteristics and trophic status (Reynolds, 1984; Harris, 1986). The recurrent character of this ordered succession of seasonal events was shown to be widespread in the 1980s by a workshop of the PEG [Plankton Ecology Group of the International Society of Limnology; (Sommer *et al.*, 1986)]. It showed that the dichotomies recorded between the seasonal changes in phytoplankton in eutrophic and oligotrophic lakes depend upon the physical environment and biotic interactions, as well as on stresses resetting the progress and/or direction of the succession.

The phytoplankton biomass of ecosystems receiving large inputs of turbulent kinetic energy, such as large lakes or oceanic basins, is strongly influenced by meteorological events (Mitchell and Holm-Hansen, 1991; Mitchell *et al.*, 1991). The seasonal successions may be a better predictor of long-term environmental changes in these systems than the more usual descriptors of biomass and productivity indices (Moline and Prézelin, 1996). An initial study of plankton successions in Lake Geneva, based on a biannual cycle (1984–1985), showed that successions in Lake Geneva were globally well described by the PEG model, despite year to year variations and some minor differences (Gawler *et al.*, 1988).

The present paper re-examines the reproducibility of plankton annual successions in this lake over a much longer time (25 years). Lake Geneva has been monitored since 1957 as part of the international programme of water protection lead by the Commission Internationale

pour la Protection des Eaux du Léman (CIPEL). The chemical properties of the lake have changed, especially the phosphorus concentrations. This rapid change was accompanied by changes in the phytoplankton composition (Anneville *et al.*, 2001).

Analysing long-term variations in seasonal successions requires a method that combines within-year and between-years analyses, especially when the long-term change in phytoplankton composition and the unequal number of samples per year complicates between-years comparisons. This problem of a simultaneous examination of a set of annual records can be solved by multi-table statistical methods [see (Coppi and Bolasco, 1989) or (Bove and Di Ciaccio, 1994) for general reviews]. They often give convergent results (Chessel and Hanafi, 1996; Pagès, 1996). The STATIS method described by Lavit *et al.* and Escoufier is most suitable for our purpose (Escoufier, 1973, 1982; Lavit *et al.*, 1994). It can detect any annual pattern common to the 25 years and determine whether this pattern is stable over time or shows stochastic or chronological fluctuations. The STATIS method has been used in several biological studies (Amanieu *et al.*, 1981; Génard *et al.*, 1994; Gaertner *et al.*, 1998; Grossi *et al.*, 1999; Licandro and Ibanez, 2000), but is rarely applied to limnology.

METHOD

Study site

Lake Geneva is a large (582 km^2), elongated, warm-monomictic deep lake (Z_{mean} = 152 m; length = 72 km; maximum width = 13 km) situated in the Alps. It lies on the border between France and Switzerland at an elevation of 372 m (Figure 1a.). Winter temperatures seldom drop below 5°C and its maximal annual mixing depth varies from 50 m to the lake bottom. Full mixing occurred only in 1979, 1981, 1984, 1985 and 1986 during the period of this study. The water temperature is strongly linked to the meteorological conditions, and Lake Geneva followed a general warming trend, despite year to year irregularities, since 1988. These were mainly a result of warmer winters and springs (unpublished data), as in other European lakes (Gerten and Adrian, 2000; Straile, 2000, 2002; Livingstone and Dokulil, 2001).

Lake Geneva underwent rapid eutrophication starting in the 1960s, the total phosphorus concentration irregularly increased from 10 µg l^{-1} to 40 µg l^{-1} and reached a maximum (90 µg l^{-1}) around 1980. A programme of reduction in phosphorus loading, initiated in the early 1970s, has resulted in a slow and irregular drop in the phosphorus concentration since 1980. It is now below 40 µg l^{-1} (Figure 2a). As a result, there have been longer periods during which the dissolved organic phosphorus in the top 10 m has been depleted, in parallel with the drop in phosphorus concentration (Figure 2b), and the depleted layer observed during the clear water-phase has extended deeper into the water column since 1988 (Figure 2c).

Phytoplankton sampling

The data used in this investigation (period 1974–1998) were obtained at the Thonon hydrobiological station with the survey programme developed by CIPEL. The survey programme started in 1957 and sampling was standardized in
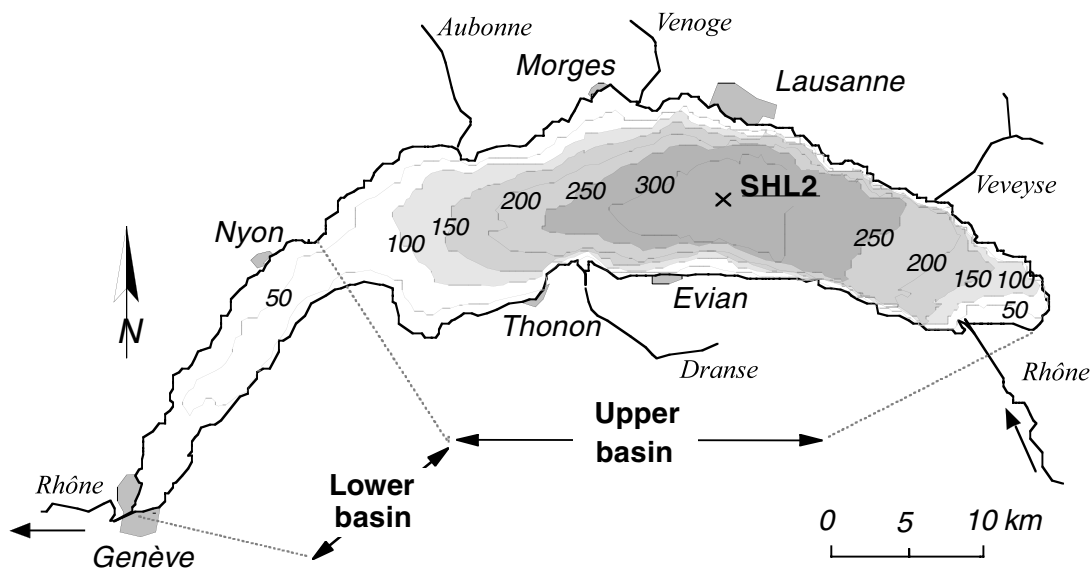

Fig. 1. Lake Geneva is situated in the Alps, on the border between France and Switzerland. Samples were taken at the centre of the Upper Basin at the reference station SHL2, midway between Evian and Lausanne.
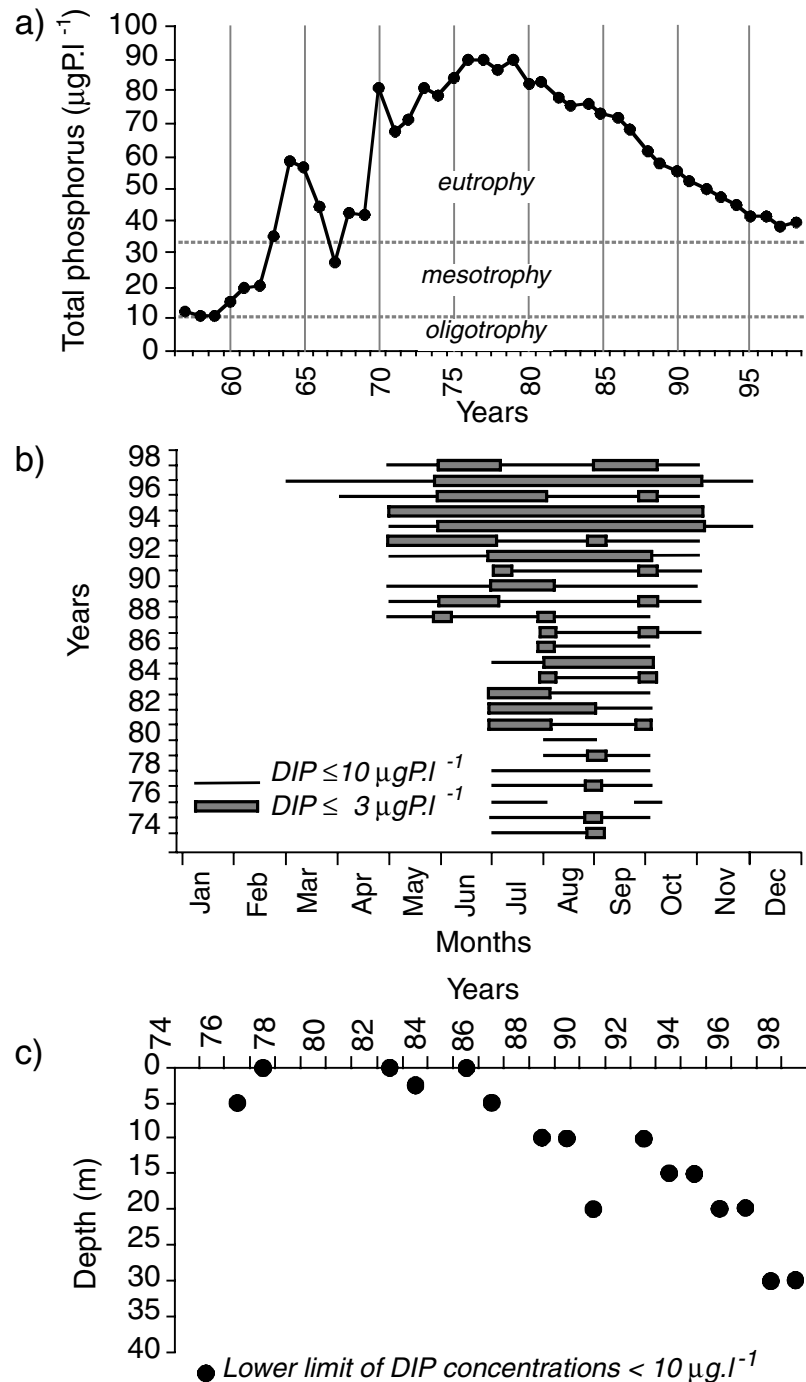
Fig. 2. Long-term trend of phosphorus concentration: (**a**) annual mean total phosphorus concentration and trophic status determined on the basis of the OCDE (OCDE, 1982). (**b**) annual and long-term changes in the duration of the period depleted of low dissolved inorganic phosphorus in the topmost 10 m of the water column. (**c**) depth of the layer depleted of dissolved inorganic phosphorus (concentrations < 10 μg P l⁻¹) during the clear water phase.

1974. The survey underwent a major revision in the sampling frequency in 1981. After this date, samples were taken twice a month during the warm season, and monthly in late autumn and winter. Data on phytoplankton species composition and biomass were regularly published in the annual reports of the CIPEL, along with other descriptors. The data used in this study are from the reference station located in the middle and deepest part of the Upper basin,

between Lausanne and Evian (Figure 1). Phytoplankton species in samples of raw water, collected in the upper 10 m with a Pelletier integrating bell (INRA patent, 1978) and preserved with Lugol's iodine, have been counted since 1974. Species were counted by the Utermöhl technique (Utermöhl, 1958) and their volumes estimated by the Lohmann method (Lohmann, 1908). The total algal biomass was then estimated by summing the volumes of each species (cell volume × cell number).

Data preparation

A total of 372 species has been identified at the reference station since 1974. However, most of them occur rarely and 162 species have only been recorded once or twice over the 25 years. These rare species may not be characteristic of the environment or may have been carried into the pelagic zone by storms. Their rarity makes them unsuitable for statistical analysis. Hence all species with an occurrence below 1% have been considered to be noise and excluded from the investigations. The results are based on the remaining 210 species and a total of 451 samples.

The exploited data have been assembled in a table of 210 columns and 451 rows (Figure 3), in which each column corresponds to a variable (species biomass) and each sample occupies one row. This table was then subdivided into 25

subsets, each corresponding to one annual survey. Species biomass is expressed in logarithmic terms to make variations in phytoplankton uniform. All the analyses were run using ADE-4 software (Thioulouse et al., 1997).

STATIS analysis

The STATIS method is based on linear algebra and especially on spaces of Euclidean vector (Escoufier, 1973, 1982; Lavit et al., 1994). STATIS is designed to study simultaneously several subsets of quantitative data and deals with the structure which is common to these different subsets. In our case, the three mean steps of this method will successively reveal (1) the proximity between years, (2) the pattern of the phytoplankton succession which repeats from one year to another, and (3) its long-term modification.

The first stage of this method is called the inter-structure analysis (Figure 3). It consists in comparing the 25 annual structures and distinguishing the years sharing a similar annual structure. Because the number of samples per subset is not equal, the dimensions of the 25 subsets are first standardized by calculating a matrix of scalar products between species for each year. Then, the calculation of a matrix of intermatrix scalar products (between years) allows comparison of the years and its diagonalization allows the representation of the proximity between years.
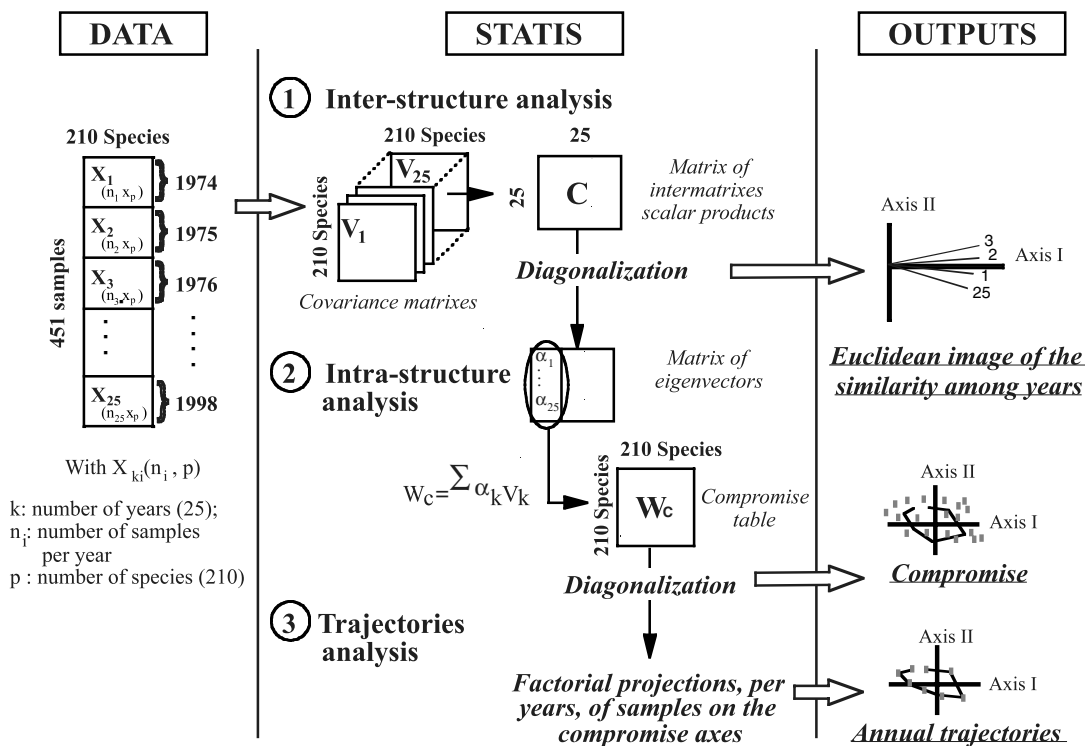

Fig. 3. Scheme of the data set and the three main steps of the STATIS method with their respective outputs.

The second step, the intra-structure analysis, involves constructing a mean table of maximum inertia (a compromise table). The 25 coefficients of the first eigenvector provided by the diagonalization of the matrix of inter-matrix scalar products are used to weight the 25 matrixes of scalar product between species. In the resulting compromise table, a greater importance is thus given to years which have similar structures. The diagonalization of this compromise table provides axes and components which express the stable part of the annual structure.

The 25 subsets are then projected separately onto the compromise in order to draw and compare the annual trajectories of the samples.

RESULTS

Analysis of the inter-structure (between-years analysis)

The representation of the first eigenvalues and eigenvectors shows the resemblance between the years based on their annual phytoplankton successions (Figure 4). The first eigenvalue coming from the inter-structure analysis is isolated from the others (Figure 4a.) and explains 31% of the total inertia. The representation of the eigenvectors on the Euclidean space (Figure 4b) shows that the 25 components (years) of the first eigenvector all have high values on axis I. Such a uniform distribution on the first axis, which explains most of the total inertia, indicates a strong common annual structure. This recurrent part of the annual phytoplankton change, which reflects the annual change in phytoplankton community structures, is the 'compromise' in STATIS analysis.

On the other axes, the inter-structure analysis emphasizes a segregation of groups of years. It indicates differences in the annual structures between years. Two groups can be seen on axis II (Figure 4b): 1988 is associated with the 1990s, with 1991 looking a little particular. The second eigenvector explains only a minor part of the total inertia (7.5%). However, such a distribution in the Euclidean space suggests the existence of two main alternatives in the annual patterns identified. The third axis explains
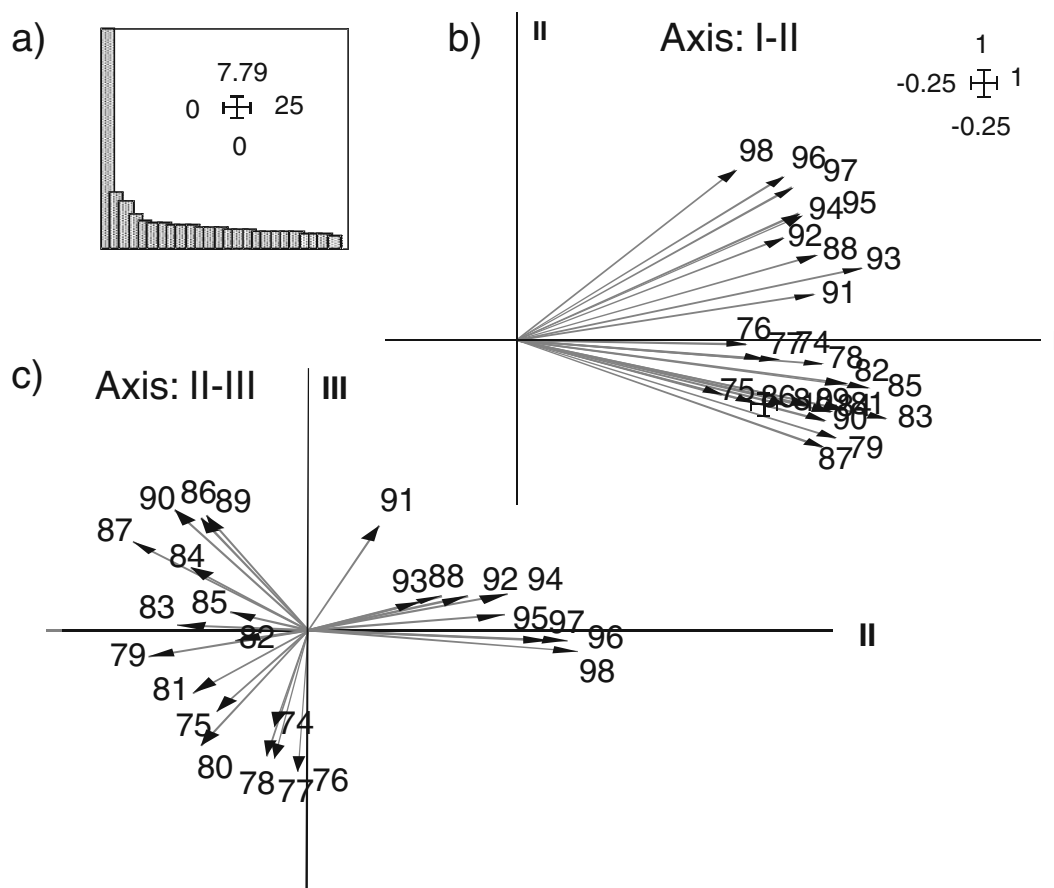

Fig. 4. Graph showing the between-structures analysis. It provides information on the similarities between the annual structures and: (**a**) eigenvalues of the inter-structure analysis, (**b**) position of the years in the first plane (axes I and II) and (**c**) position of the years on the plane defined by axes II and III.

6.3% of the total inertia. Despite a rather regular change over the years, the 1970s and 1980s may be divided into two distinct groups of years, separated by transition years. One group has negative high and low values on the third axes while the other has positive high and low values (Figure 4c.). The first group and transition years end in 1981 or 1985 (with 1979 being somewhat particular), the second one starts in 1986 and finishes in 1991 (with 1988 looking exceptional).

Thus, the inter-structures analysis shows both a strong recurrent annual structure and major alternatives distributed among chronologically organized periods. The boundaries of the period cannot be set precisely as they depend on the degree of similarity desired between the years. But we identified three groups of years. The two main groups cover 1988 plus the 1990s and the other the 1970–1980s, two other groups cover the years 1974 to around 1981 and 1986 to around 1991 (not including 1988). The inter-structures analysis does not show the nature of the compromise and provides no information on the reason for such differences and similarities between the years. We therefore carried out the intra-structure analysis.

Intra-structure analysis: the 'compromise'

The first three axes (Figure 5) only account for 31% of the total inertia, with 16% for axis I; 8% for axis II and 7% for axis III. However, given the great number of variables (210), the first three axes provide a good summary of the annual species organization over the 25 years.

The species contributing most to the annual phytoplankton structure are shown in Figure 5 and Table I. These species are distributed on the first two axes because of their pattern of annual occurrence. The projection of the samples on the Euclidean plan I–II (Figure 6) provides a graphical representation of the compromise, whose interpretation requires consideration of the correspondences with the species.

The correlation between the species and the Euclidean co-ordinates (Figure 7) allows the selection of the 24 species most responsible for the observed month distribution. As these 24 species account for the major part of the phytoplankton biomass (84% of the average phytoplankton biomass per sample), their changes can be considered to be representative. Table I shows these 24 species, and summarizes species seasonal memberships based on their positions in the Euclidean space:

The first axis of the analysis is defined by two distinct communities (Figure 5 and Figure 7). One community is dominated by nanoplankton species, mainly individual cells of Cryptophyceae (*Rhodomonas minuta*) and diatoms (*Stephanodiscus minutulus*, *S. neoastraea*) and those of the smallest species of Dinophyceae (*Gymnodinium helveticum*),

which are considered to be 'r' strategists. These fast-growing, small species are selected by strong turbulence and high nutrient concentrations (Margalef, 1958). The second community contains much larger forms, including individual species (*Ceratium hirundinella*), colonial species (*Dinobryon sociale*) and filamentous forms (*Aphanizomenon flos aquae*). These are generally considered as 'K' strategists. They have some measure of self-regulated movement, which leads to large size and relatively complex adaptive behaviours. These characteristics tend to result in low growth rates but high resistance to zooplankton grazing. These species are more strongly favoured when mixing is weaker and resources are diminished (Margalef, 1958). The projection of the months (Figure 6) shows that these two communities are separated into two sets of months: January to May with an 'r' strategist community and July to October with a 'K' strategist community. Thus Axis I separates a winter–spring community (groups G1, G2) from a summer–autumn community (groups G3, G4) in Table I.

The second axis is defined by the large species of the summer–autumn community previously defined by axis I (groups G3, G4). But these large species fall into two categories on axis II (Figure 5). Large individual motile species, such as *Peridinium willei* (significant at 1%), and to a lesser extent *Ceratium hirundinella* or *Eudorina elegans* colonies (significant at 5%) formed one group, with another community mainly represented by the largest elongated species made a great contribution to axis II (Figure 7). These latter species (*Mougeotia gracillima*, *Planktothrix rubescens*, *Diatoma tenuis* and *Closterium aciculare*) are dominated by forms without flagellae or without the ability to control their buoyancy, allowing them to move within the water column and adjust their position according to their nutrient and light needs. Thus, axis II appears to reflect a gradual change within the summer–autumn community defined by axis I. It appears to indicate a summer maturation of the community with gradual shifts toward the dominance of larger forms, characteristics of end-summer depleted waters and of rapid fluctuations of light on a well-mixed water columns. The distribution of the months confirms this interpretation as it reflects a transition from July to October (Figure 6). Axis II also shows the changes that occurred during the second half of the year and differentiates between species characteristic of the summer and autumnal community in Lake Geneva.

The third axis is defined by the small species of the winter–spring community previously defined by axis I (groups G1 and G2). It separates the insignificant species from a set of diatoms (*Fragilaria crotonensis*, *Stephanodiscus minutulus*, *Asterionella formosa*, *Fragilaria ulna* v. *angustissima*) and Cryptophyceae (*Rhodomonas minuta*). It separates a period with few phytoplankton from one having many species and
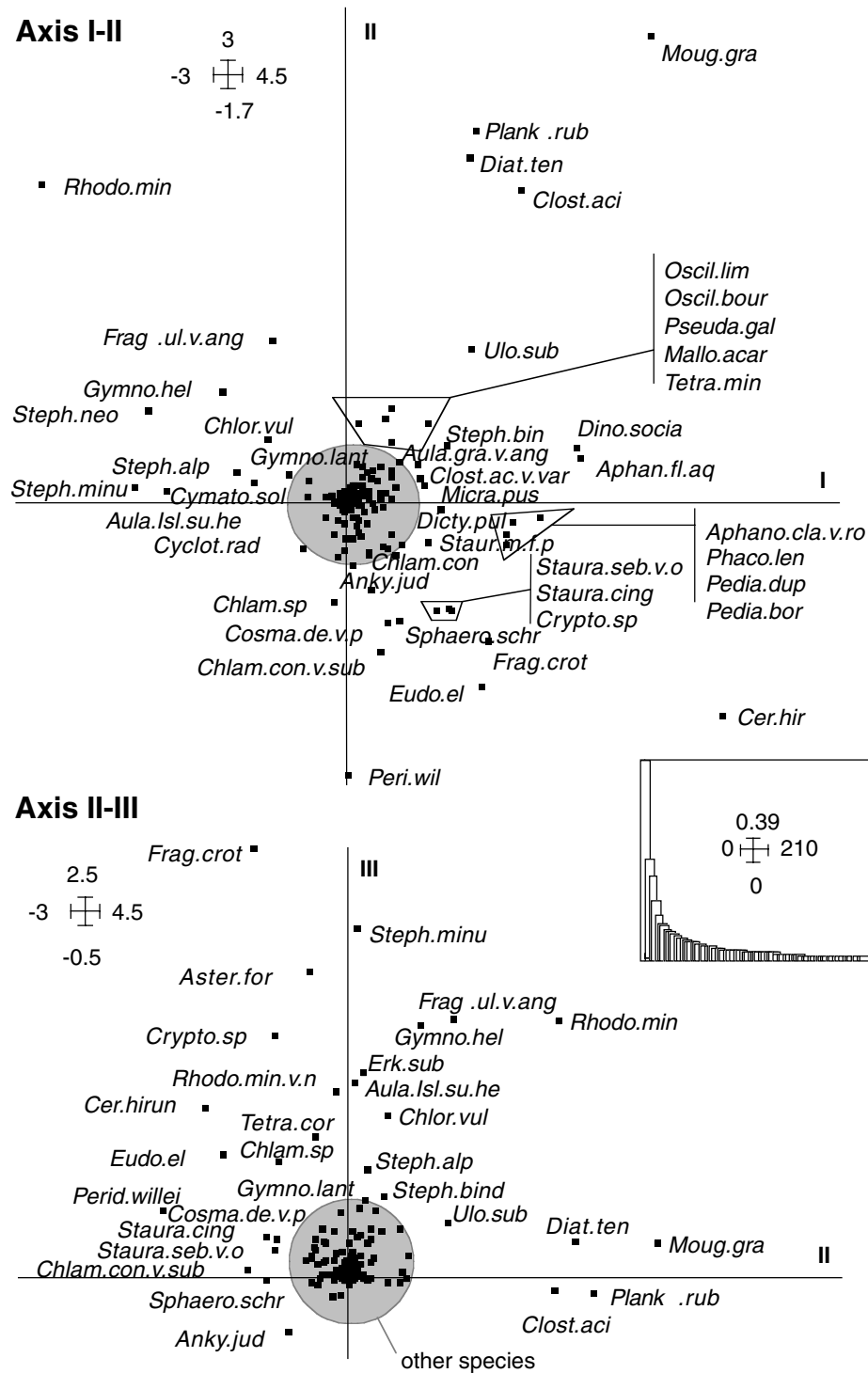
Fig. 5. Projection of the variables (species) in the first planes (axis I–II and II–III) of the compromise. Species are shown in Table I.

a community mainly composed of diatoms and nanophytoplankton (Figure 5). The correspondence with months (Figure 6) shows that axis III mainly reflected the change during the early part of the year. January and February have a poor phytoplankton community, March to May have spring species (Table I, group G2). The projection of June close to the winter months emphasizes the poor community of the well-marked clear water phase in Lake Geneva.
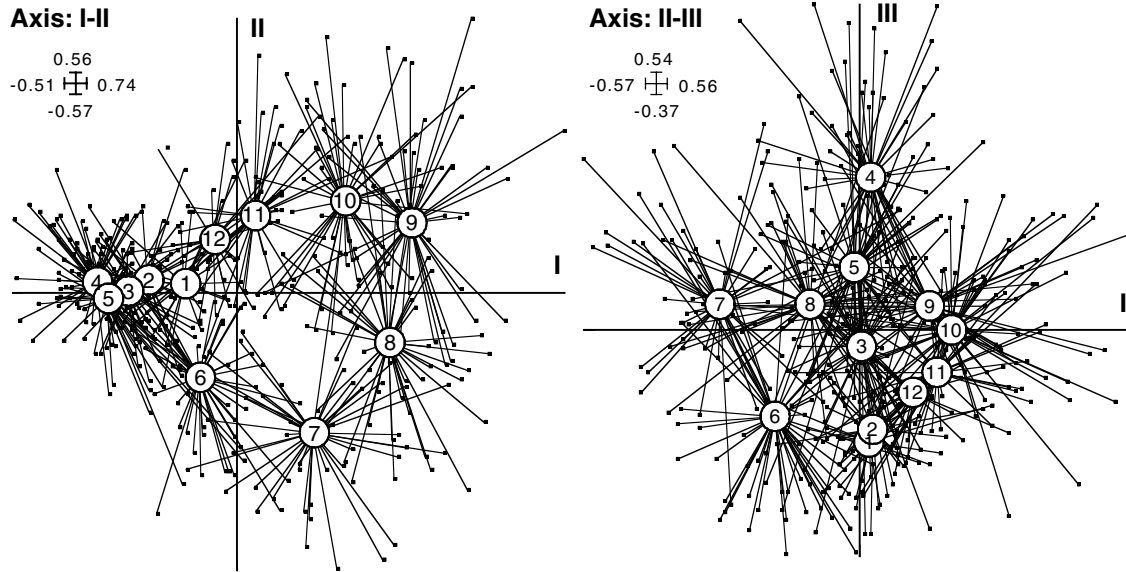
Fig. 6. Graphical representation of the compromise. Projection of all the samples (dots) and months barycentre on the planes made by axes I–II and axes I–III.
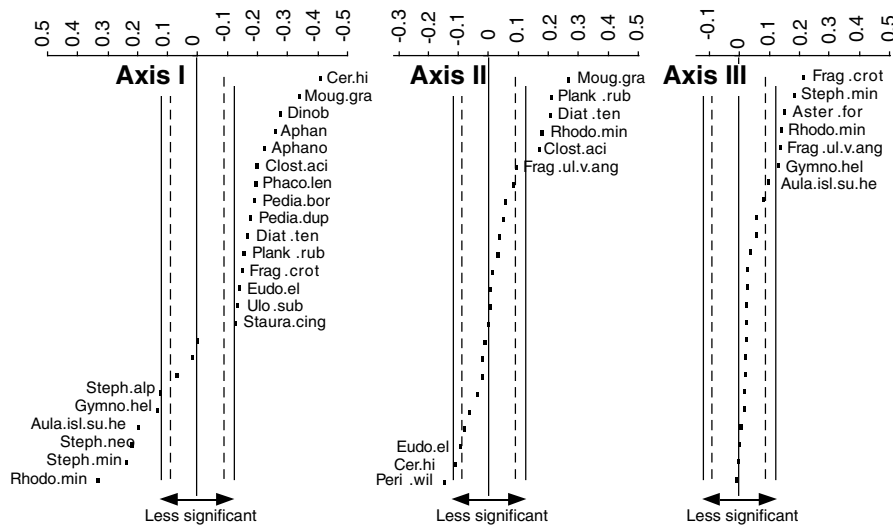

Fig. 7. Correlation between species biomass and factorial coordinates on the three first axes: 24 species were found to be significantly correlated with these axes (for $\alpha = 1\%$).

Annual trajectories on the first plane

The projection of all sample trajectories on the first plane shows the between-year distortions of annual structures versus the compromise (Figure 8a). Distortions are mainly detected on axis II, which reflects the summer changes in the phytoplankton community. We find three types of

annual structure: round, flat down-oriented and ellipsoidal up-oriented. The deformation of the mean annual structure is not randomly distributed in time. The distortions follow a chronological logic, and reveal three scenarios.

From 1974 to 1985, the annual trajectory is regular and round-shaped. Seasonal changes in the composition of the community are close to those defined by the

Table I: Characteristics of the species responsible for the observed stable part of the annual pattern

Abbrev.	Species	CLA	Axis no. (1%)	NAN	CAT	Biomass (μg l^{-1})	%
Group 1: Winter							
Steph. neo.	*Stephanodiscus neoastraea*	DIA	I	–	i	8517	1.20
Cymato. sol.	*Cymatopleura solea*	DIA	–	–	i	894	0.13
Group 2: Spring							
Rhodo. min.	*Rhodomonas minuta*	CRY	I–II–III	n	i	34,139	4.83
Rhodo. m.v.n.	*Rhodomonas minuta* var. nannoplanctica	CRY	–	n	i	28,260	4.00
Frag. crot.	*Fragilaria crotonensis*	DIA	I–III	–	c	27,097	3.83
Aster. for.	*Asterionella formosa*	DIA	I–III	–	c	22,148	3.13
Steph. min.	*Stephanodiscus minutulus*	DIA	I–III	n	i	18,126	2.56
Aula. isl.su.he.	*Aulacoseira islandica* su helvetica	DIA	I–III	–	f	12,946	1.83
Chlam. sp.	*Chlamydomonas* sp.	CHL	–	n	i	10,188	1.44
Frag. ul.v.ang.	*Fragilaria ulna* v. *angustissima*	DIA	I–III	–	i	8520	1.21
Gymno. hel.	*Gymnodinium helveticum*	DIN	I–III	–	i	6996	0.99
Erk. sub.	*Erkenia subaequiciliata*	CHR	–	n	i	5511	0.78
Steph. alp.	*Stephanodiscus alpinus*	DIA	I	n	i	5404	0.76
Chlor. vul.	*Chlorella vulgaris*	CHL	–	n	i	3693	0.52
Tetra. cor.	*Tetraselmis cordiformis*	CHL	–	n	i	1946	0.28
Gymno. lant.	*Gymnodinium lantzschii*	DIN	–	n	i	298	0.04
Group 3: Summer							
Cer. hir.	*Ceratium hirundinella*	DIN	I	–	i	125,829	17.80
Crypto. sp.	*Cryptomonas* sp.	CRY	–	–	i	44,941	6.36
Frag. crot.	*Fragilaria crotonensis*	DIA	I–III	–	c	27,097	3.83
Eudo. el.	*Eudorina elegans*	CHL	I	–	c	15,348	2.17
Staura. cing.	*Staurastrum cingulum*	CON	I	–	i	10,233	1.45
Peri. wil.	*Peridinium willei*	DIN	I–II	–	i	8285	1.17
Pedia. bor.	*Pediasatrum boryanum*	CHL	I	–	c	7910	1.12
Staur. seb.v.o.	*Staurastrum sebaldii* v. *ornatum*	CON	–	–	i	7889	1.12
Aphano. cla.v.ro.	*Aphanothece clathrata* v. *rosea*	CYA	I	–	c	6430	0.91
Chlam. con.v.sub.	*Chlamydomonas conica* v. *subconica*	CHL	–	n	i	4730	0.67
Phaco. len.	*Phacotus lendneri*	CHL	I	n	i	2832	0.40
Pedia. dup.	*Pediastrum duplex*	CHL	I	–	c	2778	0.39
Dicty. pul.	*Dictyosphaerium pulchellum*	CHL	–	–	c	1878	0.27
Staura. m.f.p.	*Staurastrum messik.* f. *planctonicum*	CON	–	–	i	1666	0.24
Cosma. de.v.p.	*Cosmarium depressum* f. *planctonica*	CON	–	–	i	1326	0.19
Chlam. con.	*Chlamydomonas conica*	CHL	–	n	i	1075	0.15
Sphaero. schr.	*Sphaerocystis schroeteri*	CHL	–	–	c	1019	0.14
Anky. jud.	*Ankyra judayi*	CHL	–	–	i	681	0.10
Group 4: Autumn							
Moug. gra.	*Mougeotia gracillima*	CON	I–II	–	f	56,236	7.95
Diat. ten.	*Diatoma tenuis*	DIA	I–II	–	i	32,288	4.57
Plank. rub.	*Planktothrix rubescens*	CYA	I–II	–	f	28,325	4.01
Clost. aci.	*Closterium aciculare*	CON	I–II	–	i	16,895	2.39

Table I: continued

Abbrev.	Species	CLA	Axis no. (1%)	NAN	CAT	Biomass (µg l⁻¹)	%
Dinob. soc.	*Dinobryon sociale*	CHR	I	–	c	16,273	2.30
Aphan. fl.aq.	*Aphanizomenon flos aquae*	CYA	I	–	f	14,972	2.12
Oscil. bour.	*Oscillatoria bourrellyi*	CYA	–	–	f	6227	0.88
Ulo. sub.	*Ulothrix subtilissima*	CHL	I	–	f	5195	0.73
Steph. bin.	*Stephanodiscus binderianus*	DIA	–	–	f	5039	0.71
Micra. pus.	*Micractinium pusillum*	CHL	–	–	c	3406	0.48
Pseuda. gal.	*Pseudanabaena galeata*	CYA	–	–	f	1417	0.20
Mallo. acar.	*Mallomonas acaroides*	CHR	–	–	i	1414	0.20
Oscil. lim.	*Oscillatoria limnetica*	CYA	–	–	f	1337	0.19
Tetra. min.	*Tetraedron minimum*	CHL	–	n	i	1051	0.15
Aula. g.v.ang.	*Aulacoseira granulata* v. *angustissima*	DIA	–	–	f	884	0.13
Clost. ac.v.va.	*Closterium acutum* v. *variabilis*	CON	–	–	i	735	0.10

Classes indicated by: CYA, Cyanophyte; DIN, Dinoflagellate; CRY, Cryptophyte; CHR, Chrysophyte; DIA, Diatoms; CHL, Chlorophyte; CON, Conjugate; Axis no., number of the axis to which the species made a significant contribution; NAN, class-size: nanoplankton (n) or microplankton (–); CAT, categories of form: unicellular (i), colonial (c) or filamentous (f); Biomass, total biomass reached over the 25 years; % = species percentage to the total phytoplankton.

compromise and the maturation of the summer community clearly separates the motile cells of Dinophyceae *Ceratium hirundinella* and *Peridinium willei* from the large elongated forms (*Mougeotia gracillima*, *Closterium aciculare* and *Planktothrix rubescens*) on axis II. The annual pattern of each seasonal group confirms that the spring algae are best represented during the early part of the year (Figure 8b). Their maximum occurs in April. A second phytoplankton bulk occurs from July to October with a maximum in August. It is composed both of summer and autumnal species. However, the summer species strongly dominate. This summer species community continues until September and then declines and is replaced by autumnal species.

From 1986 to 1991, the annual patterns are rather flat and down-oriented. The year 1988 appears to be atypical as its trajectory is similar to those of the 1990s. Spring species are still dominant during the first part of the year and reach a maximum in April. However, the second part of the year contains mainly summer species that dominated until late autumn, because of the extremely poor development of autumn species. Axis II separates mainly spring and winter species (*Rhodomonas minuta*, *Stephanodiscus neoastraea*, *S. minutulus*, *Aulacoseira islandica* sub. *helvetica* and then *Planktothrix rubescens*) from summer species (*Ceratium hirundinella*, *Aphanothece clathrata* v. *rosea*, *Peridinium willei*). Thus, the maturation of the summer community towards large forms that usually occur in autumn, is not well pronounced during this period.

From 1992 to 1998, the structure has an ellipsoidal and up-oriented shape, except for 1993 when it is more round than ellipsoidal but still up-oriented (Figure 8a). The spring community reaches a maximum in April and decreases more markedly than in the previous periods. A second phytoplankton bulk occurs from July to late autumn (Figure 8b). Axis II separates *Mougeotia gracillima*, *Diatoma tenuis*, *Planktothrix rubescens*, *Closterium aciculare* (autumn species) and *Peridinium willei* (summer species), marking the strong, rapid maturation of the summer community. The annual pattern (Figure 8b) indicates that summer species are not the main ones of the summer community, in contrast to the two previous periods. The summer community is dominated by summer species only in July, the autumn species, which are already present in July, then become dominant in August and continue until late autumn.

DISCUSSION

Model for seasonal changes in Lake Geneva

The compromise for Lake Geneva is built upon the organization of a pool of 24 species representing an average of 84% of the phytoplankton biomass in each sample. This annual pattern fits well with the common

annual succession in phytoplankton composition described by the PEG model (Sommer *et al.*, 1986), but for the first half of the year only. The model does not provide as good a fit during the second half of the year.

Seasonal dynamics during the first half of each year

As in the PEG model, the most characteristic species of this period in Lake Geneva are diatoms and Cryptophyceae (G1: winter and G2: spring, Table I). They are generally fairly small species (nanoplankton), but larger ones such as *Stephanodiscus neoastraea*, *Asterionella formosa* and *Gymnodinium helveticum* are not excluded. These species are commonly compared with 'r' strategists or invasive strategists and renamed competitors by Reynolds (Reynolds, 1993, 1997). They are considered to have a high growth rate even at low or variable light intensities and their morphology provides a high surface : volume ratio, enabling rapid nutrient exchange through the cell surface (Reynolds, 1984). The changes in phytoplankton during this first half of the year fall into four stages:

December to March (winter and the beginning of spring)—Low temperature, high nutrient concentration and unstable water column. Abiotic factors, such as light intensity, temperature and mixing, are the major limiting factors during this period, as in other deep lakes (Sommer *et al.*, 1986). These environmental conditions are probably more suited to species that tolerate physical perturbations or even species requiring turbulence to remain in suspension.

April—Strong development of G2 species. Their growth coincides with the onset of the stratification that appears in March (Pelletier and Blanc, 1991) and their maximum generally occurs in April.

May—Zooplankton grazing and decrease in silicate concentration. This gradually leads to another form of community that is characteristic of June.

June—Very species poor phytoplankton community. This is the 'clear water phase' (Gawler *et al.*, 1987; Balvay, 1997). The water column stratification increases and the nutrient concentrations begin to fall. The development of a strong thermocline reduces exchanges with the metalimnion and the euphotic zone becomes nutrient-depleted. Autogenic factors become more important during this period (Sommer *et al.*, 1986) and the environment selects for better 'competitors' for the limiting resource.

Seasonal dynamics during the second half of the year

There is a great functional diversity, with both small species (*Chlamydomonas conica* v. *subconica*, *Phacotus lendneri*, *Ankyra judayi*) and large ones, which are the main contributors to the phytoplankton biomass (*Aphanothece clathrata* v. *rosea*, *Dinobryon sociale*, *Mougeotia gracillima*, etc.).

These species (groups G3 and G4 in Table I) are more efficient at exploiting the scarce resources and conserving rather than propagating their biomass. They are called 'stress-tolerant species' (S) by Reynolds (Reynolds, 1988) and compared to the 'K' strategists. These species are usually large individual cells or colonies, motile or buoyant, growing relatively slowly and having relatively high nutrient storage capacities. In Lake Geneva there is a simple maturation pattern during this period, instead of the four main steps described in the PEG model (ie. Chryptophyceae and green-algae; large diatoms; dinoflagellates or Cyanophyceae; nitrogen fixing species):

July to August—The most representative species are *Peridinium willei* and *Ceratium hirundinella*. These dominate the summer biomass and last until late summer; they were responsible for the high phytoplankton biomass observed in 1975 and 1976 (Anneville *et al.*, 2001).

September to October—There is a transitional period that leads to an autumnal community that may last until November. This autumnal group of species (G4) includes mainly filamentous algae (*Mougeotia gracillima*, *Planktothrix rubescens*) whose morphological and functional properties make them close to 'K' strategists. They start to develop in early summer, in parallel with the development of the early-summer species. Since they are better adapted for autumnal conditions (deepening of the mixed layer, decreasing vertical temperature gradient and light intensity), they become dominant in October. Diatoms become increasingly important as autumn progresses and the community gradually shifts to the winter species.

Long-term modification of the annual structure

Our second purpose was to determine whether the annual structure was stable throughout the 25-year study. The results of the inter-structure analysis revealed three groups of years, the 1970s and 1980s opposed to the 1990s plus 1988, and 1974 to 1981 separated from the last years of the 1980s (Figure 4). Analysis of the annual trajectories on the first plane showed a clustering of the years almost identical to that of the inter-structure analysis (Figure 8): a group including the 1970s and 1980s (from 1974 to 1985), a second one including the 1990s plus 1988, and an intermediate one including the years from 1986 to 1991 (except 1988). The small differences between the inter- and intra-structure clustering are a result of the fact that the inter-structure analysis looks for the overall similarities between years, whereas the intra-structure analysis focuses only on the first plane. It does not take into account the variations defined by the other axes, which also contribute to the overall variability. However, because there is a strong similarity between the inter- and intra-structure clustering, we can state that the pattern described by axis
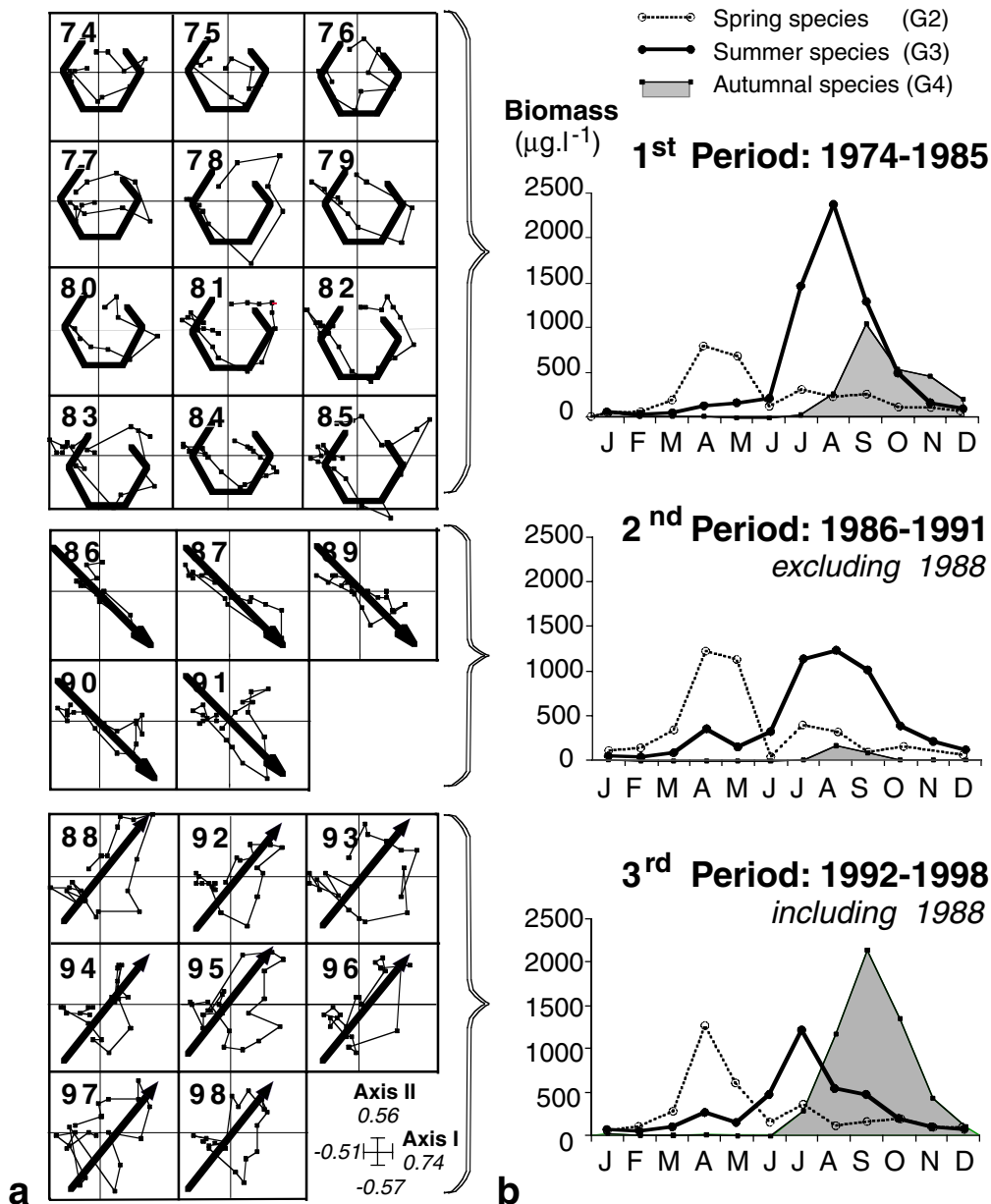
Fig. 8. (**a**) Long-term distortion of the annual structure shown on the first plane (axis I–II): three types of structure were identified: regular and round shaped, flat and down-oriented, ellipsoidal and up-oriented. (**b**) Annual changes in spring, summer and autumn species based on the median biomass (seasonal pattern of species were from the within-structure analysis, see in Table I).

II is one of the main sources of the between-year variations underlined by the inter-structure analysis. Hence, we can now focus on the first plane (axes I and II), which gives a functional interpretation of the differences between years, which the inter-structure analysis could not do.

The study of the annual changes on the first plane revealed three kinds of annual patterns reflecting functional changes in the system. These three annual patterns fall into three distinct periods (Figure 8):

First period (1974 to 1985)

The annual structure is close to the previously defined compromise. This period is rather long (12 years) and there is no atypical year. From meteorological and physico-chemical points of view (Monod *et al.*, 1984; Anneville and Pelletier, 2000), successive years are different and there was full winter mixing in some of them (1979, 1981, 1984, 1985). Hence, different environmental

features give the same annual structure. The annual pattern is stable and the results show that the system is able to persist despite environmental disruption and changes. This characteristic of ecosystems, called resilience by Holling (Holling, 1973) and resistance by Pimm (Pimm, 1984), is usually expressed using quantitative units such as density or biomass. We show in this study that it is also possible to express resistance directly in term of a graphical pattern reflecting the link between seasonal changes.

Second period (1986 to 1991)

There was a sudden shift in the annual structure in 1986, and another period of resistance despite changes in the environmental conditions. During this period, there was no summer maturation and no characteristic 'pre-autumnal' community. The year 1988 is exceptional in that it had a different annual structure, very close to that of the third period. This shows that, despite its resistance, the system can suddenly switch from one annual structure to another. It emphasizes that the resistance is not an intrinsic property of the system, but results from the succession of several interacting mechanisms, which may lead to similar patterns of succession, but more extreme changes may lead to a sudden shift.

Third period (1992 to 1998)

The annual structure was similar to that of the year 1988. Thus, 1988 appears to be a precursor year. The factors responsible for such a sudden change in 1988 may have also determined the annual structure during 1992–1998. The most striking difference from the two previous annual successions is a summer community dominated not by summer species, but by autumnal ones. During this third period, the annual changes in the species succession occur earlier. There is an early decrease in summer species in favour of autumnal ones. Then, the 'pre-autumnal' population becomes dominant sooner in the year (July and August).

Variations in the timing of the seasonal events have been shown to be linked to changes in climate (Müller-Navarra *et al.*, 1997). The third period recorded in Lake Geneva coincides with the world-wide warm period and an extreme phase of the North Atlantic oscillation that is believed to be a major source of variations in weather and climate in the northern hemisphere (Hurrel, 1995; Hurrel and Loon, 1997). Climate affects the timing of processes at different trophic levels (George and Harris, 1985; Eckman *et al.*, 1988; Karentz and Smayda, 1998; Straile and Adrian, 2000; Gerten and Adrian, 2000). As a consequence, the material and energy flow through the system (match/mismatch of seasonal events) is perturbed and the patterns of phytoplankton succession may be altered. The first appearance of the third annual structure in 1988

coincided not only with higher temperatures but also with an earlier depletion of the phosphorus concentration. The warmer winters and springs that have occurred since 1988 may have favoured spring phytoplankton growth. As a consequence, combined with the general decrease in phosphorus concentration, phosphorus limitation started earlier in the year. The scarce nutrient conditions that generally occur at the end of summer, therefore appeared earlier in the first 10 m, whereas there was still sufficiently phosphorus deeper, where light becomes the main limiting factor, to ensure strong phytoplankton growth. Such environmental conditions may favour species adapted to low light intensity and thus the installation of a community usually characteristic of late summer and autumn. Since these species are large and poorly grazed by zooplankton, they may accumulate and lead to a greater biomass than that of the summer species. This may explain the annual structures in 1988 and from 1992 to 1998. However, since 1989, 1990 and 1991 were similar to 1988 on the basis of phosphorus but had different annual structures, phosphorus alone did not lead to the annual change.

CONCLUSION

The STATIS method can be used to reveal the annual mean stable pattern of seasonal changes in the phytoplankton community and underlines the inter-annual modifications of the seasonal structure. In Lake Geneva, the annual mean stable pattern mainly reflects the succession of phytoplankton communities characteristic of cold (winter–spring) and warm (summer–autumn) periods.

By contrast, the monthly changes within these two distinct cold and warm periods were distorted from one year to another. These distortions in the annual structure were not random, but reflect a long-term change in the functioning pattern of the whole system: the system was resistant to environmental changes and suddenly switched from one mode of functioning to another. It is difficult to prove that this change lies along an oligo-trophic–eutrophic gradient alone, or was linked to changes in meteorological conditions. Nevertheless, we believe that the timing and the severity of the phosphorus limitation could be a major cause of changes in the annual structure of phytoplankton. But these changes may also result from factors or, more probably, sets of factors, that act on a longer time scale than the short-term perturbations or the seasonal ones. The links between environmental parameters and the annual phytoplankton structure must be identified to give a better understanding of the factors responsible for such long-term changes in the annual pattern of phytoplankton. This will be the purpose of further studies.

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