Long-term changes in the copepod community of Lake Geneva

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Lake Geneva is a deep, peri-alpine lake where there has been a continuous monitoring program since the 1970s. The lake has long suffered from eutrophication. In the early 1980s, a restoration plan resulted in a progressive reduction in the phosphorus concentration. During the same period, the lake responded to large-scale climate changes by overall warming of the water, and changes in the timing of stratification. Both the composition and the phenology of the plankton have been affected. This paper focuses on the long-term changes observed in the copepod community. Our findings highlight a switch towards a copepod community dominated by calanoids. In addition we have detected a period (1986 to 1991, 1988 excluded) characterized by an unusual seasonal pattern of species succession. It is suggested that these changes have been induced by qualitative changes in the phytoplankton community, and underline fluctuations in trophic interactions between planktonic species. Re-oligotrophication and warming, therefore, emerge as indirect forcing factors, and these findings contribute to the debate about whether copepods can be used as indicators of environmental changes.

INTRODUCTION

Long-term changes in the abundance of copepods in marine ecosystems have been widely documented (Dippner *et al.*, 2001; Beaugrand *et al.*, 2002; Chiba *et al.*, 2006). In limnic ecosystems, similar investigations have mainly focused on cladoceran species. *Daphnia*, the key-stone genus in the ecology of standing waters, has been the most studied herbivore in lake plankton and has been shown to be a useful indicator of large scale climatic events (Straile, 2002). Less attention has focused on freshwater planktonic copepods, which play an important and complex role in the trophic dynamics of aquatic ecosystems. They contribute to the nutrition of planktivorous fish and feed on a wide range of organisms from phytoplankton and protozoans to small zooplankton. Therefore, they can influence the structure of plankton communities through selective predation, as is the case of cyclopoids (Chang and Hanazato, 2005). Calanoids in turn have a more herbivorous diet and compete with the early copepodite stages of cyclopoids.

Copepod life cycles have different stages whose ecology and sensitivity to environmental pressures (food, predation, etc.) varies according to the species. As a consequence, the steepness of the response to environmental change is species-specific, which results in different dominance patterns. Accordingly, cyclopoids appear to be indicators of climate change (Gerten and Adrian, 2002). They are also sensitive to food availability being dominant in eutrophic lakes, whereas calanoids appear less sensitive to food availability and are usually more abundant than cyclopoids in oligotrophic lakes (Sommer and Stibor, 2002).

The role planktonic copepods play in the ecology of lakes, as well as their sensitivity to environmental changes makes this group a suitable biological model to investigate changes in aquatic ecosystems and food–web interactions. In the present study, we investigated the interannual and seasonal changes in the copepod community of Lake Geneva during the period 1974–2004. This lake was eutrophic by the end of the 1970s. In the mid 1970s, the development of sewage treatment

with iron, an awareness campaign targeting farmers, and a ban on detergents containing phosphates in Switzerland were some of the successful measures that have reduced external phosphorus loading and the restoration of mesotrophic conditions (Anneville, 2001). Moreover, Lake Geneva has been also affected by large-scale meteorological forcing (Anneville *et al.*, 2002b), and deep water temperatures have increased (Lazzarotto *et al.*, 2004), probably as a result of the climate warming observed at the global scale.

While previous studies in Lake Geneva have highlighted the response of phytoplankton assemblages (Anneville *et al.*, 2002a, b), rotifers (Molinero *et al.*, 2006) and fish communities (Gerdeaux and Dewaele, 1986; Gerdeaux, 2004; Gillet and Quetin, 2006) to environmental changes, little attention has been paid to medium-sized zooplankters such as copepods. Our main goals were to analyse long-term trends and potential phenological changes in the copepod community and to try to identify the forcing factors responsible for such changes. The results are discussed in the context of the possible use of plankton populations as indicators of limnic environmental variability.

METHOD

Sampling

Lake Geneva is one of the largest lakes in Western Europe (surface area: 582 km^2, maximum depth:

309 m), and it is of special value for fishing, recreational activities, and water-use. The economic importance of Lake Geneva has lead to the implementation of a monitoring program instigated by an International Committee for the Protection of Lake Geneva (CIPEL). Monitoring started in 1957, and was standardized in 1974. Our sampling was carried out as part of this lake monitoring program.

Samples were collected once a month from 1974 to 1981 and twice a month thereafter at a sampling station situated in the middle of the upper basin (Fig. 1).

Hydrological data. Water-temperatures were measured and water samples were collected for the estimation of dissolved inorganic phosphorus concentrations from a series of depths from the surface to the lake bottom. Values used correspond to the mean water temperature measured in the 0–50 m depth layer. From 1974 to 1998, the temperature was measured with a thermometer, and thereafter a multiparameter probe (CTD90) for oceanic and limnological measurement of physical, chemical and optical parameters was used. There was a period of three years (1995 to 1998) during which these two techniques overlapped. During this period, the average difference between the values recorded was 0.07°C, and the maximum temperature difference was 0.59°C. For the subsequent analyses of the temperature data, thermometer measurements were used till 1998. The dissolved inorganic phosphorus concentration was measured using acid molybdate (AFNOR, 1982).

Biological data. Phytoplankton was sampled in the top 10 m from 1974 to 2001, and then in the top 20 m.
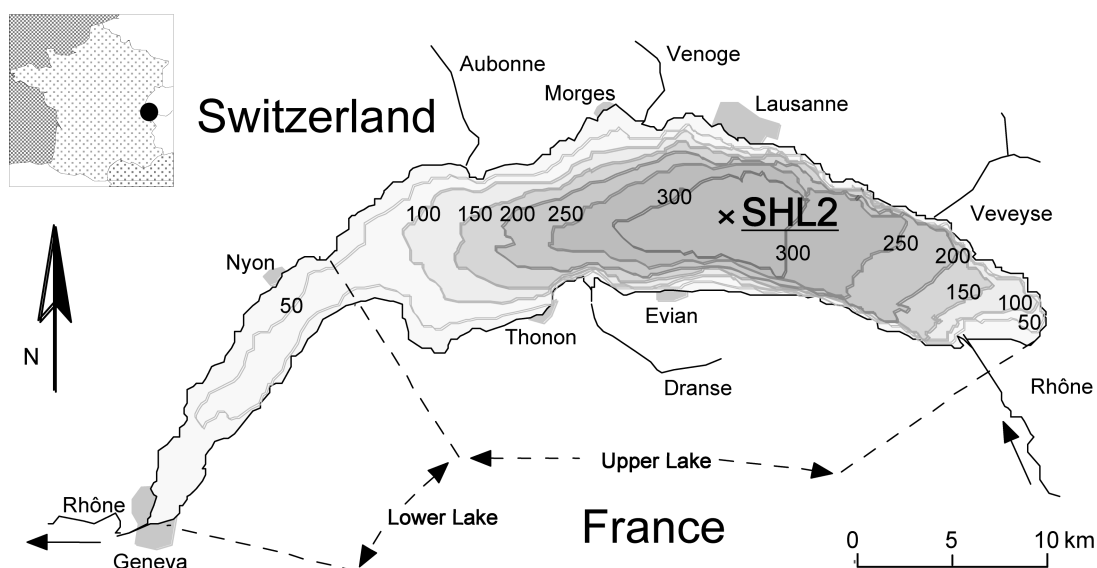
Fig. 1. Bathymetric map of Lake Geneva indicating the position of the sampling station (SHL2).

Phytoplankton samples were collected using an integrating sampler (developed by J.P. Pelletier at the INRA station of Thonon Les Bains). The samples were immediately preserved with Lugol. Zooplankton was collected using a 200 μm mesh net during vertical tows from 50 m to the surface. These samples were immediately preserved in formalin for use in the abundance estimations.

Phytoplankton identifications and counts were carried out in sedimentation chambers under an inverted microscope (Utermöhl, 1958). Species biovolumes were calculated from cell numbers and mean cell volumes using geometrical models. The total biomass was then estimated by adding the biovolumes for each species, assuming a fresh weight of 1 g cm^{-3}. The phytoplankton was sorted into two categories on the basis of size. The first category that of the 'Nanophytoplankton', includes organisms less than 50 μm long and with a biovolume smaller than 10 000 μm^3. All the other phytoplankton species were assigned to the 'Microphytoplankton' category.

Zooplankton from a sub-sample was counted and identified under a dissecting microscope. Copepod developmental stages were systematically identified. From 1974 to 1984, identification was carried out to the family level; this was increased to species level from 1984 to 2004.

Data analyses

Data analyses consisted of three main steps as follows
First step. The average annual phosphorus concentration data come from Lazzarotto *et al.*, (2004). Long-term changes in water temperatures were investigated by analysing temperature anomalies. Anomalies were computed for each month, using the monthly means from a transformed matrix as the reference values. The matrix was transformed in order to eliminate irregularities due to missing values and unequal numbers of samples. The transformation consisted of a linear interpolation to the 15th of each month. The monthly reference values were computed for the period 1974−2004. The interpolation was also applied to the matrices of phytoplankton and zooplankton abundances in order to obtain one value per month. Annual averages were then calculated from the monthly data.

Second step. Statistical analyses of the data were run using ADE4 software. Because of the high number of variables in our dataset, a multivariate method was applied. In order to be able to distinguish the influence of inter-annual fluctuations on the variability of the copepod community from the seasonal ones, we used a 'between-group' approach (Dolédec and Chessel, 1989). A between-group principal component analysis (BGPCA) was applied to the abundance data (Thioulouse *et al.*, 1997). The method is adapted to analyse matrices where the objects are gathered by group (Dolédec and Chessel, 1989) and its goal is to focus on between-group variability. The BGPCA is equivalent to a principal component analysis run on the weighted average of each group. It seeks for axes of the centre of gravity space and focuses on the between-group difference. For this study, the objects of the matrix were gathered by years in order to focus on the between-year variability.

From 1974 to 1983, taxonomic identification was carried out at the family level and thereafter at the species level. Consequently, we performed two consecutive analyses. The first analysis covered the period from 1974 to 2004, and the second that from 1984 to 2004. In both studies, the data matrix was constructed using the zooplankton taxa as variables (column) and sampling dates as the objects (rows). In the first analysis (1974−2004), the zooplankton taxa were divided into eight groups corresponding to the following developmental stages for both calanoids and cyclopoids: nauplii, early copepodites (C1−C3), late copepodites (C4−C5) and adults. In the second analysis (1984−2004), we considered nine variables, corresponding to late stages (copepodites C4 to adults) of the nine species listed in Table I. The abundance data were log-transformed and standardized per column at zero mean and unit variation. In both matrices, the sampling dates were grouped by year. As a consequence, focusing on the between-group variability highlights the inter-annual changes. The statistical significance of the dispersal of the centres of gravity was tested using the permutation test provided by the ADE4 software. The tests were run with 10 000 permutations.

The link between inter-annual changes and environmental parameters was demonstrated using a discriminant analysis. The six quantitative descriptors used in this analysis to explain the grouping of the years are the annual mean water temperature, the dissolved inorganic phosphorus concentration, the nanophytoplankton and microphytoplankton biomass, and the abundances of carnivorous and herbivorous Cladocera.

Third step. The abundance ratio of the main plankton categories was computed for each sample, and plotted as a temporal map in which the ordinates are the succeeding years, and the abscissas correspond to the successive sampling days during the year. This representation gives an overall view of the seasonal and inter-annual changes in the seasonal phenology. It makes it possible to identify characteristic periods.

Table I: Copepod species observed in Lake Geneva

Species	Family	Order	Size (mm)	Freq. (%)	Abund. × 10³ ind.m⁻²	Contr. (%)
Eudiaptomus gracilis (Sars, 1863)	Diaptomidae	Calanoida	M: 1.00 − 1.20 F: 1.20 − 1.50	100	47820	63
Cyclops vicinus (Ulianine, 1875)	Cyclopidae	Cyclopoida	M: 1.15 − 1.50 F: 1.25 − 2.18	87.3	14433	19
Cyclops prealpinus (Kiefer, 1939)	Cyclopidae	Cyclopoida	F: 1.40 − 1.65	99.7	9979	13
Cyclops strenuus (Fischer, 1851)	Cyclopidae	Cyclopoida	M: 1.20 − 1.76 F: 1.46 − 2.30	5.4	122	0.16
Acanthocyclops vernalis (Fischer, 1853)	Cyclopidae	Cyclopoida	M: 1.00 − 1.20 F: 1.00 − 1.80	0.5	*0.48*	*0.001*
Acanthocyclops robustus (G.O. Sars, 1863)	Cyclopidae	Cyclopoida	M: 1.00 − 1.10 F: 1.30 − 1.40	26.4	3961	5
Acanthocyclops gigas (Claus, 1857)	Cyclopidae	Cyclopoida	M: 2.00 − 2.50 F: 2.00 − 4.00	3.9	2	0.002
Mesocyclops leuckarti (Claus, 1857)	Cyclopidae	Cyclopoida	M: 0.80 − 1.00 F: 0.90 − 1.30	8.5	41	0.054
Macrocyclops albidus (Jurine, 1820)	Cyclopidae	Cyclopoida	M: 1 − 1.30 F: 1.70 − 2.50	1.6	5	0.006

The sizes of the individuals are indicated for Males (M) and Females (F) according to Dussart (1967, 1969). Frequency of occurrence (Freq), abundance (Abund.) and contribution to the total abundance (Contr.) have been computed for the period from 1984 to 2004.

RESULTS

Changes in abiotic and biotic environmental parameters

The annual average of dissolved inorganic phosphorus concentration peaked in 1977, and remained around 74 μgP L⁻¹ until 1979 (Fig. 2A). The phosphorus concentration then started to decrease, and had fallen to 26 μgP L⁻¹ by 2004.

Water temperature records from 1974 to 2004 indicate that Lake Geneva experienced strong interannual fluctuations, the amplitude and nature of which varied
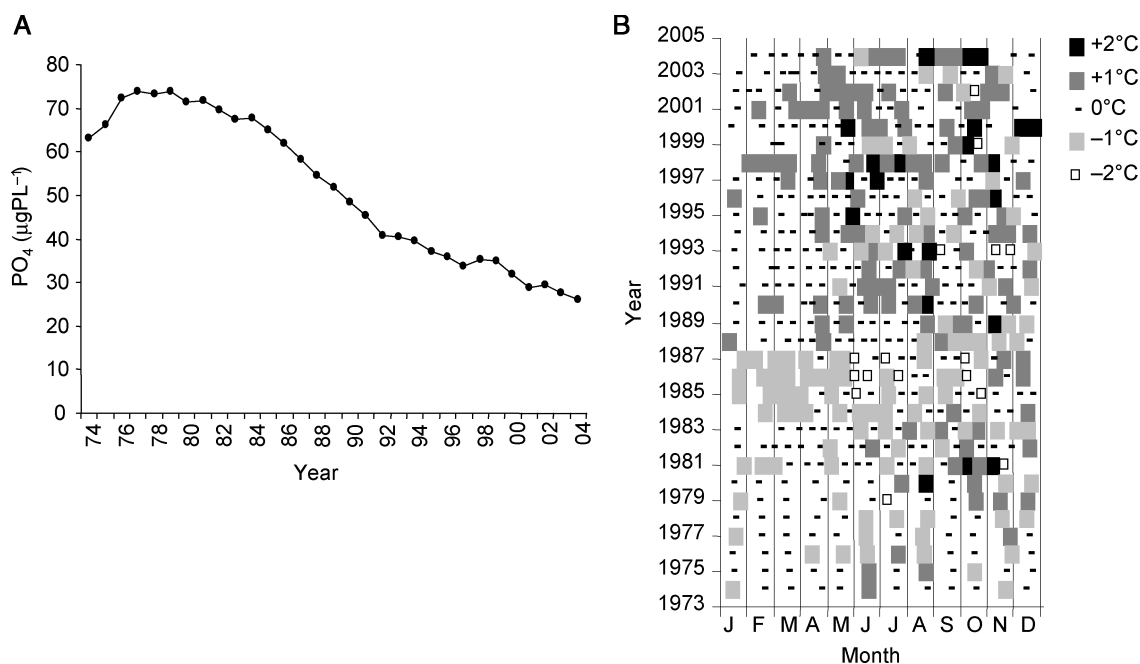

Fig. 2. Long-term changes in the dissolved inorganic phosphorus concentration and water temperature: (**A**) Long-term changes in the annual mean weighted concentration of dissolved inorganic phosphorus (Lazzarotto *et al.*, 2004). (**B**) Sequence of water temperature anomalies. Anomalies are the departures of the water temperature, measured in the first 50 m, from the long-term monthly mean computed for the period 1974−2004.

over the course of the year. The temporal sequence of water temperature anomalies reveals a cold period from 1984 to 1987 (Fig. 2B). In contrast, temperatures have tended to be higher than the monthly average in spring and summer since 1988 (Fig. 2B).

In addition to these abiotic changes, Lake Geneva has shown a marked long-term trend in phytoplankton biomass (Fig. 3) with biomass increasing from the early 1990s. This increase is a result of proliferation in micro-phytopankton, whereas the nanophytoplankton shows a decreasing trend over the same period.

Herbivorous cladocerans are dominated by the genus *Daphnia*. After a slight increase in the abundance of this category of zooplankton, a downward trend has been observed since 1986. This decrease has been accompanied by an increase in the carnivorous clado-cerans, *Leptodora* and *Bythotrephes*. In contrast, despite strong inter-annual fluctuations, the abundance of cope-pods does not show any clear trend. In Lake Geneva, the copepod community is mainly dominated by a

single calanoid species: *Eudiaptomus gracilis* (Table I) and eight cyclopoid species of which *Cyclops vicinus* and *C. prealpinus* are the most abundant. *E. gracilis* is a frequent and abundant species that accounts for up to 63% of the total abundance measured from 1984 to 2004. *Acanthocyclops robustus* occurs occasionally (in 26% of the samples) and makes only a small contribution to the total abundance (5%). The other cyclopoid species (*C. strenuus*, *A. vernalis*, *A. gigas*, *Mesocyclops leuckarti* and *Macrocyclops albidus*) are rare. Analyses of taxon abun-dance have highlighted long-term changes in the com-position of the copepod community, and some inter-annual changes in the seasonal pattern of species dominance.

Long-term changes in the copepod community

The projections of the years 1974 to 2004 onto the 2 first axes obtained with the BGPCA are shown in
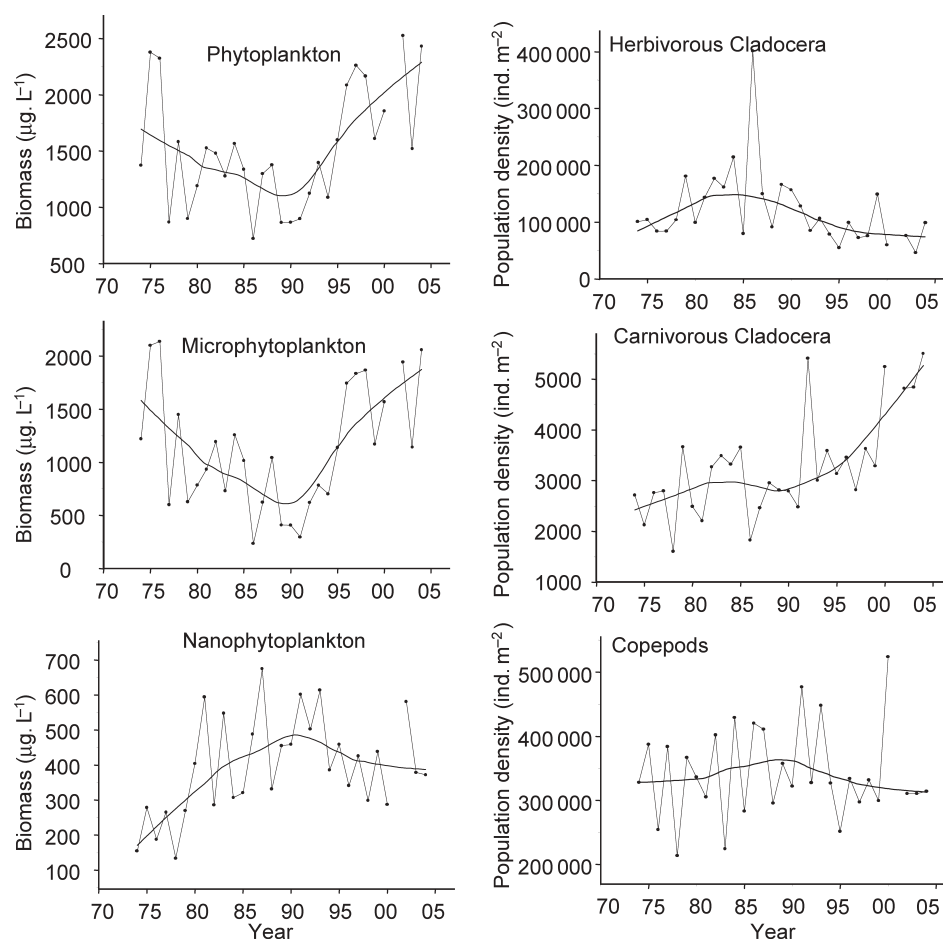
Fig. 3. Long-term changes in biotic environmental parameters (black circles). The general trends of the time series are obtained by Loess smoothing (black line).
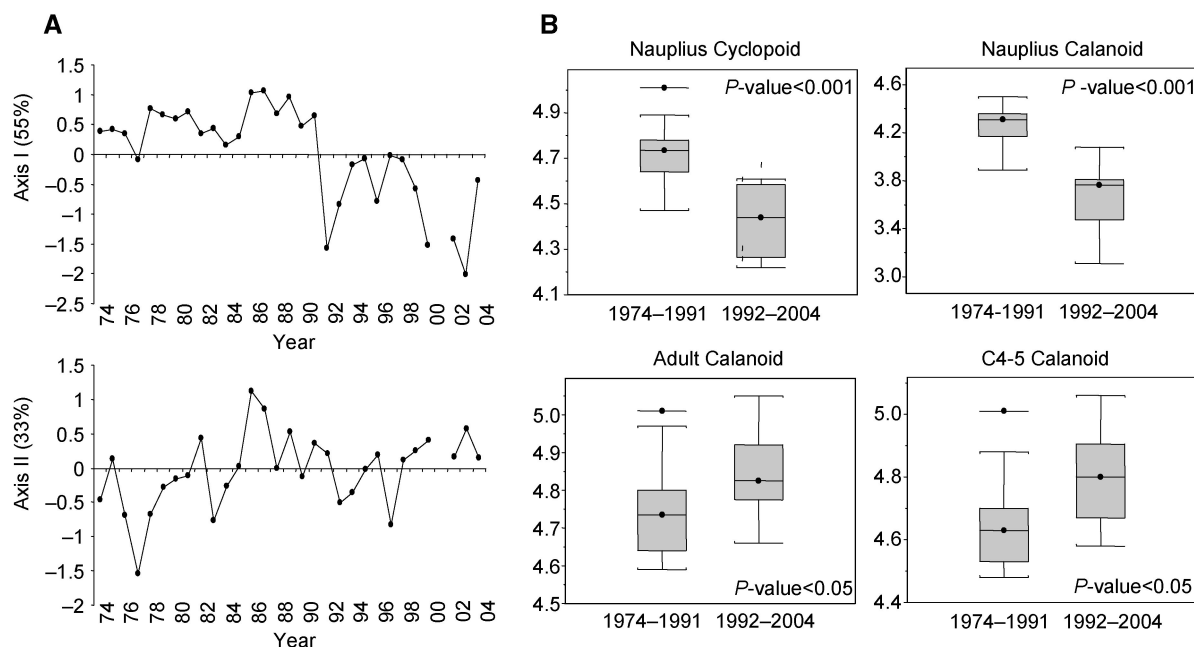
Fig. 4. BGPCA on the period 1974–2004: (**A**) Scores of the barycentre for successive years on axis I and axis II. The percentage of inertia explained by each axis is indicated in parentheses. (**B**) Comparison for the two main periods identified on axis I, of the abundances of cyclopoid nauplii, calanoid nauplii, calanoid adults and calanoid C4-5.

Fig. 4A. Axis II accounts for 33% of the total variability and highlights irregular inter-annual fluctuations. Axis I, which accounts for 55% of the variability, reveals the differences between two periods. The first period consists mainly of the 1970s and 1980s, and the second of the subsequent years, the switch-over occurring in 1992. The zooplankton taxa that contribute to the formation of axis I are the nauplii of calanoids and cyclopoids, they account for 40 and 16% of this axis, respectively. These categories characterize the first period. Adult and C4–5 calanoids are also important contributors to axis I (20 and 18%, respectively), and they characterize the second period. Indeed, in recent years, the abundance of nauplii has been significantly lower for both calanoids and cyclopoids. In contrast, the abundance of the later stages of calanoids has increased in recent years (Fig. 4B).

BGPCA carried out over a shorter period (1984–2004) and with better taxonomic identification highlights a long-term trend on axis I, which accounts for 39% of the total inertia (Fig. 5). However, in contrast to the previous analysis, this trend can be divided into three periods: the first one (from 1984 to 1990) is characterized by *Acanthocyclops robustus*, *C. vicinus* and *C. strenuus*, which contribute 23, 20 and 12%, respectively, to the formation of axis I; an intermediate period from 1991 to 1997, and a third period (1998 to 2004) characterized by *C. prealpinus* (26%) and the calanoid *Eudiaptomus* (14%). A discriminant analysis, run on the

previously described environmental parameters, has been used to determine which environmental variables best accounted for differences between the three time-periods identified by the between-group analysis. The environmental parameters identified as the main explanatory descriptors were the dissolved inorganic phosphorus concentration, then the annual mean water temperature, carnivorous cladoceran abundance and, to a lesser extent, microphytoplankton abundance. The abundance of microphytoplankton has been significantly higher in recent years (Wilcoxon-test: p-value < 0.005) in contrast, no difference in nanophytoplankton abundance can be observed between the periods 1984–1990 and 1998–2004 (Wilcoxon-test: p-value > 0.1).

Inter-annual changes in the seasonal dynamics of the copepod community

Long-term changes in the ratio between the abundances of calanoids and cyclopoids indicate a progressive increase in the contribution of calanoids to the copepod community (Fig. 6A). Furthermore, the pattern of dominance between calanoids and cyclopoids displays consistent seasonal changes (Fig. 6B). Cyclopoids are more abundant in spring, when the dominant species is *C. vicinus* (Fig. 6D), whereas calanoids are more abundant in summer. There have been two main
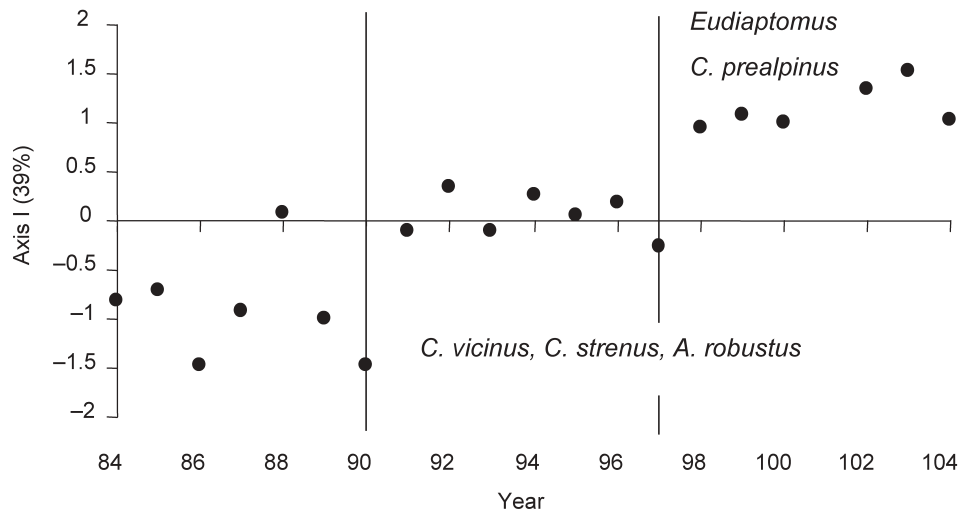
Fig. 5. BGPCA for the period 1984-2004: Scores of the barycenter for the years on axis I. The percentage of inertia explained by the axis, and the main species contributing to its formation are indicated.

discontinuities in this pattern. The first occurred in the late 1980s. From 1986 to 1989, with the exception of 1988, cyclopoids proliferated to an unusually high level compared to the other years. Consequently, cyclopoids were dominant from the end of summer till the end of the year (Fig. 6B). A more detailed analysis of the species composition revealed that this period coincided with a high abundance of *A. robustus* (Fig. 6D). From 1986 to 1990 (1988 excluded), this species was a large component of the total copepod community (Fig. 6C). During this period, monthly medians of its relative abundances fluctuate between 26% (in July) and 70% (in September). *A. robustus* was absent in most of the other years (Fig. 6C). The second anomaly is the disappearance of the seasonal pattern of alternating dominance of calanoids and cyclopoids. Since 2001, calanoids have dominated the community all year round. This change in the pattern of annual succession also appears in cyclopoid species. *C. prealpinus*, which was primarily a summer and autumn species, has been dominant all year round since 2002.

Long-term changes in the ratio between the abundances of nanophytoplankton and microphytoplankton indicate a progressive decrease in the contribution of nanophytoplanktonic species to the phytoplankton community (Fig. 6E). Comparison with the phytoplankton composition underlines striking synchronicity in the seasonal pattern and its inter-annual shifts (Fig. 6F). Phytoplankton succession is characterized by the alternation of small phytoplanktonic forms that dominate in spring, and the large microphytoplanktonic forms that are more abundant from summer till the end of the year. As in the copepod community, a long-term deviation from this annual pattern can be observed. Since the year 2000, the period during which small species predominate has become shorter. We have also noticed a dominance of nanophytoplanktonic forms in late summer during the years 1986–1989, with the exception of 1988. During that period, the median abundances of nanophytoplankton biomass observed in July and August were higher than those reported for the other years, but the differences between these two periods were not significant. In contrast, in September and October nanophytoplankton biomass was significantly higher (Wilcoxon test: p-value < 0.001) during the years 1986–1989 (1988 not included) than during the other years. *Daphnia*, the dominant herbivorous cladoceran, was present all year round. However, the temporal sequence of *Daphnia* abundances shows strong seasonal variations (Fig. 7). The highest abundances usually occurred in the spring. In the 1990s, this period began as early as May, and it is short because *Daphnia* abundance declined during the summer. From 1984 to 1989, maximum abundances occurred in June, and abundances continued to be high until late in September, resulting in significantly higher mean summer abundance compared to the period 1990-2004 (p-value < 0.005). During that period, the *Daphnia* population was thus maintained from July till September.

DISCUSSION

Lake Geneva has undergone marked changes over the past three decades. Monthly temperature anomalies
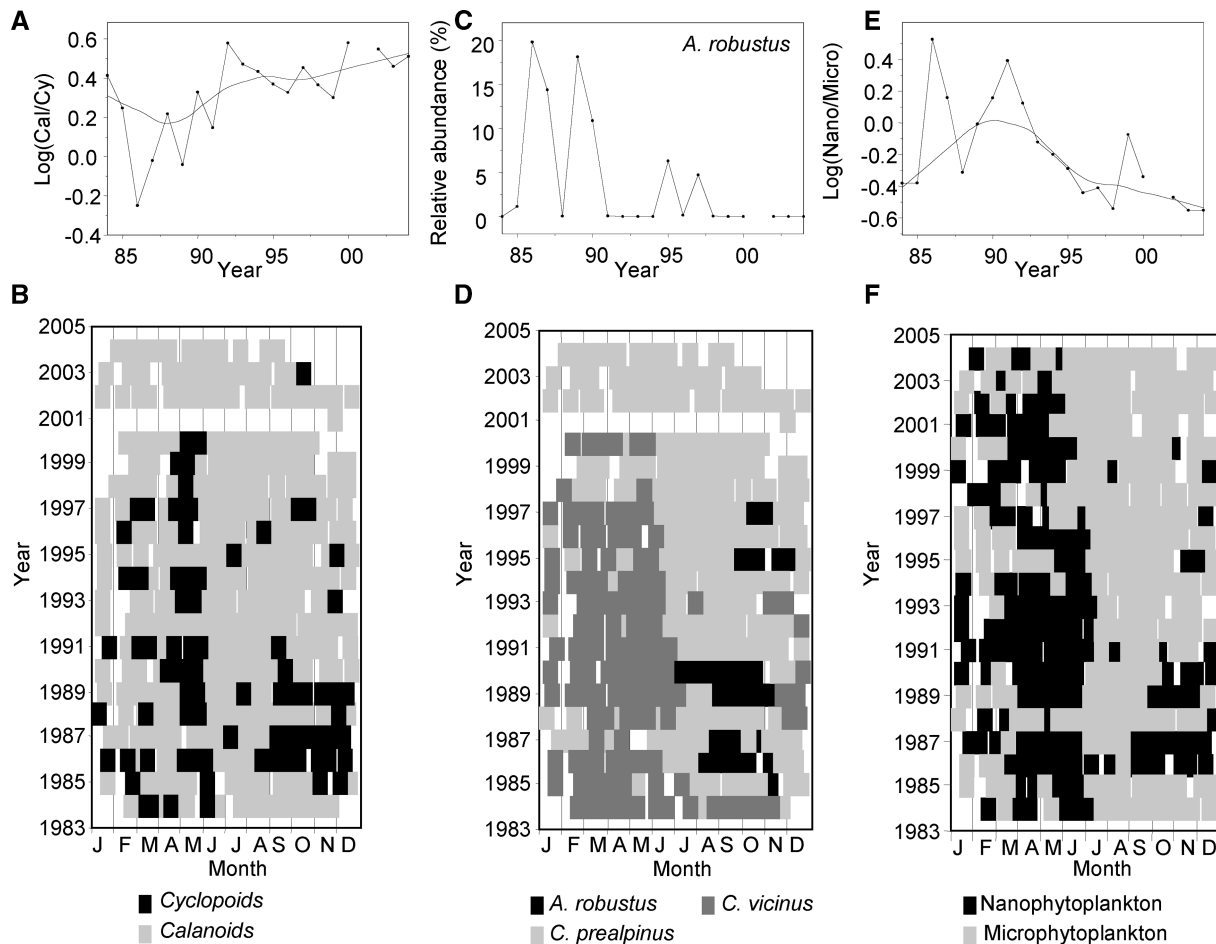
Fig. 6. Upper panels: long-term changes (black circles) and general trends obtained by Loess smoothing in the: (**A**) average ratio between the abundance of calanoids and cyclopoids, (**C**) average relative abundance of *A. robustus* and (**E**) average ratio between nanophytoplankton and microphytoplankton biomass. Lower panels: temporal maps describing seasonal and inter-annual changes in: (**B**) the ratio between calanoids and cyclopoids indicating a community dominated by calanoids (grey squares) or cyclopoids (black squares), (**D**) the dominant copepod species and (**F**) the ratio between nanophytoplankton and microphytoplankton

indicate fluctuations throughout the year until 1984-1987, when temperature values for all months were lower than the long-term means. From 1988, the values for all months have been higher than the long-term means. Changes in the water temperature together with the increase and then decrease in phosphorus concentrations have led to marked changes in the phenology and composition of the phytoplankton community (Anneville *et al.*, 2002a, b). The findings reported in this paper indicate that changes in the dynamics and composition of the copepod community have also occurred. Our results reveal shifts in their seasonal patterns, and a long-term trend in the composition of the copepod community.

Shifts in the seasonal patterns. The replacement of copepod species shows a seasonal pattern, with cyclopoids dominating in spring and the calanoid

Eudiaptomus gracilis in summer. This general pattern holds for many central European lakes where cyclopoids exploit favourable conditions during the spring outburst of nanophytoplankton to grow and reproduce. The dominant species during spring is *C. vicinus*, which is considered to be an opportunistic species (Brandl, 1998a). Its life cycle strategy allows this species to go into diapause in summer, but summer generations are not rare in eutrophic lakes (Maier, 1998). In Lake Geneva, *C. vicinus* has been recorded throughout the year, but displays marked seasonal cycles characterized by very low abundance in the summer and autumn, when the cyclopoid community is dominated by *C. prealpinus*.

Deviation from the previous seasonal pattern has been observed in the second half of the 1980s. This coincided with a characteristic seasonal pattern in the
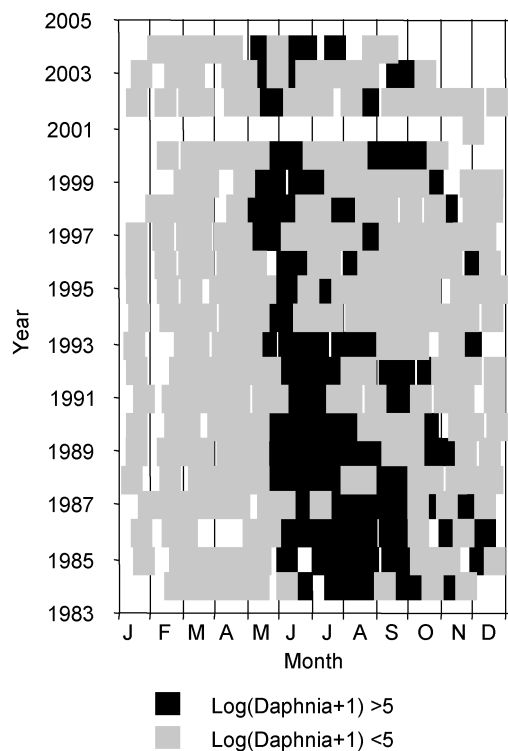
Fig. 7. Temporal map describing the seasonal and inter-annual abundances of the cladoceran *Daphnia*. Abundances are expressed as the logarithm of the number of individuals per m^2.

phytoplankton community (Anneville *et al.*, 2002a), and is one that prevails during relatively cold years. From 1986 to 1991 (with the exception of 1988), there was no summer development of the phytoplankton community, the characteristic pre-autumnal species were rare, and summer species continued to dominate until late autumn. The results reported here indicate that the nanophytoplanktonic forms were also more abundant than usual during this period. An anomaly in the seasonal pattern was also observed at the level of the overall zooplankton community (Anneville, 2001). The striking fact is that in all the trophic compartments considered (phytoplankton, the overall zooplankton community or the copepods), the year 1988 did not fit into the abnormal period. 1988 was a transitional year in terms of both temperature and phosphorus concentration. Indeed, the years have been warmer since 1988, and the annual depletion of dissolved inorganic phosphorus has occurred earlier, and extended further down the water column (Anneville *et al.*, 2002a, b). The consequences of these changes were apparent in 1988 as a modification in the phytoplankton phenology, but this disruption was not repeated in the subsequent years, and plankton dynamics returned to its former seasonal pattern. This dynamic is consistent with the phenomenon of resilience that is reported in lakes subject to environmental changes.

Seasonal changes in food availability can influence the seasonal succession of zooplankton species. In summer, cyclopoids are known to be limited by low food availability, which can restrict their population growth or even trigger diapause in some species (Santer and Lampert, 1995; Hansen and Hairston, 1998). Cyclopoid species have been reported to differ from each other with regard to their diet, predatory abilities (Brandl, 1998b), life history characteristics and sensitivity to fish predation (Maier, 1998). The summer in the second half of the 1980s, was characterized by exceptionally high abundance of the cyclopoid *A. robustus*. This species grows and reproduces in summer under the poorer feeding conditions in many central European lakes (Hopp and Maier, 2005); its success in the pelagic zone of eutrophic lakes is however reduced when fish predators are abundant (Maier, 1998). As shown by our results, herbivorous *Daphnia*, which are usually dominant in late spring, were present in large numbers in summer from 1984 to 1989. Competition for resources by herbivorous zooplankton presumably increased in July and August when the phytoplankton community was dominated by microphytoplanktonic species (Fig. 6F). Lower food requirements of *A. robustus* nauplii compared to the other cyclopoids (Hopp and Maier, 2005) might thus be an advantage for this species. Furthermore, *A. robustus* females are smaller in size but have large egg sacs. This morphological characteristic makes them vulnerable to predation by fish (Maier, 1998). No fish abundance information is available for the study period: however, fish stomach content analyses in Lake Geneva indicate that Cladocera are the main diet of fish, with *Daphnia* being preferred compared to cyclopoids (Ponton, 1986; Gerdeaux *et al.*, 2002). High abundances of *Daphnia* in the summer of the second half of the 1980s could therefore have reduced the potential predation pressure on *A. robustus*. Reduced fish predation has probably contributed to the establishment of a population of *A. robustus* which has taken advantage of the switch towards a nanophytoplankton dominated phytoplankton community in late summer. The presence of more edible phytoplankton during late summer of the second half of the 1980s in Lake Geneva (Anneville *et al.*, 2002a) could therefore promote faster growth and higher survival of the juvenile stages of cyclopoids and favour the development of large populations of cyclopoids. In turn, the predation pressure exerted by cyclopoids on calanoids should regulate the calanoid population and result in a community dominated by cyclopoids (Fig. 8).
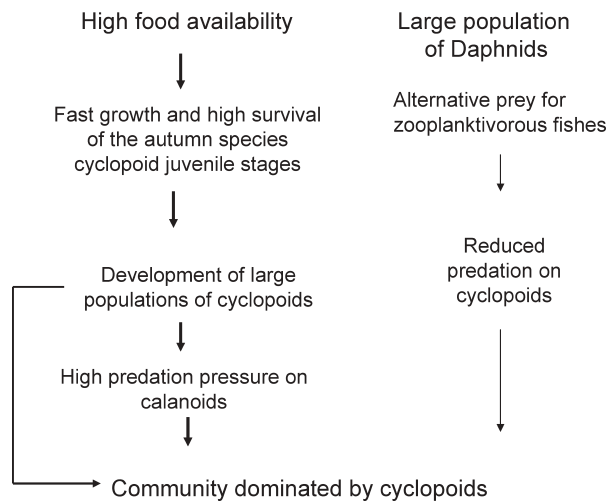
High food availability

↓

Fast growth and high survival
of the autumn species
cyclopoid juvenile stages

↓

Development of large
populations of cyclopoids

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High predation pressure on
calanoids

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Large population
of Daphnids

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Alternative prey for
zooplanktivorous fishes

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Reduced
predation on
cyclopoids

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Community dominated by cyclopoids

Fig. 8. Conceptual diagram showing the changes observed in the seasonal dynamics of the copepod community of Lake Geneva during the period 1986–1989 (with the exception of 1988).

Long-term trend in the composition of the copepod community. Over the long-term, the changes in the annual dynamics reported here appear to be indicative of structural modifications within the copepod community, mainly characterized by the increased dominance of *E. gracilis*. This trend is obvious whatever the level of taxonomic resolution and the length of the study period, only the timing of the shift differs. Eutrophication of lakes is often associated with a shift in abundance from calanoids to cyclopoids, and the establishment of large populations of *C. vicinus* (Einsle, 1983). Conversely, an increase in calanoids could indicate lake recovery and the return to oligotrophic conditions. The dominance of calanoids in oligotrophic water is attributed to reduced predation pressure from cyclopoids, which are affected by high nauplii mortality due to low algal densities (Santer, 1994). Furthermore, calanoids can survive long-term food shortages because of their low metabolic rate (Lampert and Muck, 1985). However, these mechanisms cannot explain these changes in Lake Geneva, since phytoplankton biomass increased while phosphorus concentrations were falling. The high phytoplankton biomass is due to an increase in the number of large phytoplankton. These species are poorly grazed by zooplankton and this suggests a decrease in the quality of food for zooplankton in Lake Geneva. In both calanoids and cyclopoids, the nauplius stage is a critical period in relation to food requirements and constitutes a developmental bottleneck. There is a high degree of overlap in the food requirements of these two groups; as a result, we should expect competition for the available resources between these two taxa. Unfortunately, there is not much experimental evidence

for competition between cyclopoids and calanoids *in-situ*. The food threshold required for the development of cyclopoid copepods is however much higher than that for calanoids (Santer, 1994). Accordingly, cyclopoids can be expected to be more sensitive to low food quantity or quality. Slow growth and poor survival of their juvenile stages may prevent the development of a large population, thus reducing the predation pressure on calanoids, and leading to a dominance of calanoids. We therefore suggest that in Lake Geneva, any change in food quality may initially have a direct effect on the outcome of competition between calanoids and cyclopoids.

In conclusion, our data give an integrated picture, and lead us to propose conceptual models summarizing the ecological processes that account for the long-term changes in the copepod community in Lake Geneva. Phosphorus appears to be an important environmental forcing factor, and its influence may be mediated through phytoplankton composition. Indeed, composition and dynamics of the copepod community is affected by interspecies competition and selective predation pressures, but they also appear to be very sensitive to changes in phytoplankton composition, as shown here. Despite the web of interactions between the various components of the ecosystem that buffer and introduce time-lags in the responses, copepods can be considered to be good indicators of environmental changes in Lake Geneva.

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