



Seasonal and interannual variability of cladoceran communities in two peri-alpine lakes: uncoupled response to the 2003 heat wave.

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1 **Seasonal and interannual variability of cladoceran communities in two peri-alpine lakes:**
2 **uncoupled response to the 2003 heat wave.**

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15 **Key words:** climate, heat wave, population dynamics, zooplankton, long-term changes

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Abstract

Seasonal and interannual dynamics of cladoceran species were analyzed during the period 1995-2003 in two deep peri-alpine lakes morphologically different but subjected to similar regional climatic forcing. The seasonal succession of cladoceran species was characterized and the impact of extreme climatic events on the annual pattern of species succession was assessed. Using a multivariate method, we show that the cladoceran species display marked seasonality patterns that differed in the two lakes. The differences observed between the lakes were driven by their trophic state, the plankton species composition and the abundance of predators. We show that the sensitivity of the annual pattern of species succession to extreme weather changes, illustrated by the 2003 heat wave, differs markedly in these two lakes. In Lake Annecy, the annual pattern of cladoceran succession observed in 2003 is not different from the one usually observed. In contrast, in Lake Geneva, the annual pattern recorded in 2003, is unusual and characterized by the maintenance of herbivorous cladocera during summer. These findings underline the need to consider the morphology of lakes and trophic state in the assessment of ecological responses to global warming. Our results contribute to the debate about the predictability of the impacts of climate change on aquatic ecosystems, and their extrapolation from one site to another.

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1 Introduction

2 The composition of plankton communities displays marked seasonality that has been
3 documented in both phytoplankton and zooplankton for different types of lake morphology and
4 trophic states (Sommer et al., 1986; Hart, 2004; Abrantes et al., 2005). This pattern of plankton
5 species succession is driven by interacting forces primarily physical changes, resource availability
6 and interactions between the species present (Sommer et al., 1986; Hart, 2004; Abrantes et al.,
7 2005). Water temperature is one of the main factors affecting the seasonality in species composition
8 of lakes. Thermal changes may affect plankton both indirectly, through environmental changes (e.g.
9 stratification), and directly, through their physiology (e.g. growth rate) and behaviour. This may
10 result in population size changes that can be large enough to be detected over prolonged time scales.
11 Thermal forcing has also been shown to drive the timing of the spring proliferation of cladocerans,
12 which in turn can be used as a proxy for climate-driven changes in pelagic ecosystems (Straile et
13 al., 2003). Despite the existence of species-specific responses and adaptations to water temperature
14 (Gerten and Adrian, 2002), regional-wide climate variations can synchronize the dynamics of some
15 taxa in different lakes leading to consistent regional changes in freshwater ecosystems over a
16 prolonged time scale (Rusak et al., 1999; Straile and Adrian, 2000). This has been shown in
17 European lakes for *Daphnia*, and subsequent studies in different lakes have also found that the
18 abundances of other cladoceran species are related to the North Atlantic Oscillation (Straile et al.,
19 2003).

20 In recent years, growing evidence has shown that climate variations significantly affect
21 plankton phenology, trophic interactions, food-web structure and possible ecosystem-level changes
22 (Gerten and Adrian, 2002; Straile et al., 2003; Winder and Schindler, 2004; Edwards and
23 Richardson, 2004). These observations have been supported by experimental studies (McKee et al.,
24 2002; McKee et al., 2003). However, most of the investigations have focused on keystone species,
25 and the impact of climate variability on the patterns of annual cladoceran succession remains poorly
26 documented. It is against this background that we report here an investigation of the phenology of
27 the cladoceran community in two neighbouring deep lakes that differ in their size and trophic state
28 (Table 1). These two lakes have both been subjected to similar meteorological forcing (Molinero et
29 al., unpublished data). The analysis covers a 7-year period, which includes the exceptional weather
30 conditions of 2003 associated with the exceptional heat wave in Central Europe (Schär et al., 2004).
31 In this paper, we aim to characterize the annual dynamics and potential synchrony between
32 variations in the cladocerans in Lakes Geneva and Annecy, and to assess the effect of the 2003
33 summer heat-wave on the annual pattern of cladoceran succession. The results are discussed with
34 regard to the potential consequences of extreme weather events on freshwater ecosystems.

Method

Study site and sampling - Lakes Geneva and Annecy are large and deep peri-alpine lakes about 80 km apart. They differ in their size and trophic state (Table I). According to the Organisation for Economic Co-operation and Development (OECD) criteria, based on phosphorus concentrations, Lake Geneva can be classified as a eutrophic/mesotrophic lake, whereas Lake Annecy is oligotrophic. The long-term survey program for these lakes includes bimonthly or monthly sampling to determine physical and chemical parameters and plankton abundance. A single sampling station is located in the middle of each lake, where they are deepest. As a consequence, spatial variability within each lake cannot be taken into account. The long-term survey in Lake Geneva started in the 1970s, and that in Lake Annecy started in the mid-1990s. In this study we focused on the period 1995-2003, when both lakes were being sampled. The zooplankton data for 2001 was not available for Lake Geneva, and so data for this year has been excluded from the analysis for both lakes.

Daily air temperatures were obtained from the long-term monitoring program database "ORELacsAlpins" of the French National Institute for Agricultural Research (INRA). Temperatures were measured at the INRA meteorological station located by Lake Geneva. Medians of air temperature were computed for each month and monthly values were averaged by season. For the analysis, only winter season (from January to March) was considered.

Biological data – The sampling protocol was the same in the two lakes. Zooplankton was sampled in the first 50 m using a 200 µm plankton net. This sample was preserved in a 5% buffered formaldehyde solution. Zooplankton identification and counting was carried out in one sub-sample, using a dissecting microscope. Zooplankton taxa present were counted and identified to species level. The most abundant cladoceran species found in both lakes were taken into consideration for the analysis. Individuals of *Daphnia galeata* and *D. hyalina*, were pooled, as were those of *Eubosmina longispina* and *E. mixta*, due to the difficulty of differentiating reliably between these pairs of species. The analyses were therefore performed on the following 5 groups: *Daphnia longispina*, *D. galeata* + *hyalina*, *E. longispina* + *mixta*, *Leptodora* and *Bythotrephes*.

Phytoplankton data was available from 1995 for Lake Geneva, and from 1997 for Lake Annecy. Phytoplankton was sampled using a Pelletier integrating apparatus (developed by J.P. Pelletier at the INRA station of Thonon Les Bains, INRA patent, 1978). Details of the phytoplankton sampling procedure have been published elsewhere (Anneville and Pelletier, 2000). A water sample for species identification and biomass estimation was taken from the 0-10m depth

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3 1 layer from 1995 to 2001, and from the 0-18m layer in 2002 and 2003. Similar techniques were used
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5 2 in the earlier and later phytoplankton samples. The sample was fixed with Lugol's iodine, and the
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7 3 species present were identified and counted under an inverted microscope. The laboratory
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9 4 procedure followed the standardized Utermöhl technique (Utermöhl, 1958; AFNOR, 2006). Species
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11 5 biovolumes were derived from cell numbers and mean cell volumes using geometrical models
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13 6 (Lohmann, 1908). The total biomass was then estimated by adding the biovolumes for each species,
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15 7 assuming a fresh weight of $1\text{g}\cdot\text{cm}^{-3}$. The phytoplankton species were divided into two groups
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17 8 according to size: nanoplankton (length of the cell or colony $<50\ \mu\text{m}$ and volume $<10\ 000\ \mu\text{m}^3$),
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19 9 microplankton (length of the cell or colony $>50\ \mu\text{m}$ and volume $>10\ 000\ \mu\text{m}^3$).

20 10 **Physical and phosphorus data** - Temperatures were measured every meter along a vertical
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22 11 profile from the surface to a depth of 50m using a multiparameter probe ME (Standart-ECO-Probe
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24 12 Version II) up to 2001 and then by a CTD 90 multiparameter probe Sea-Sun Tech. A stratification
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26 13 index was computed for each sampling date. This is equal to the maximum difference in water-
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28 14 temperature per meter. Two temperature time-series data were used for the analysis, each of them
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30 15 corresponding to the phytoplankton and zooplankton found in the sampled depth-layers of 0-10 m
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32 16 and 0-50m, respectively. Samples for phosphorus determination were collected at discrete depths
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34 17 ranging from the surface to the bottom of the lake. The water was sampled using home made Van
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36 18 Dorn type bottles. The total phosphorus concentration was measured by a spectrophotometric
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38 19 method with Ammonium Molybdate according to AFNOR 1982, NF EN 1189 (Murphy and Riley,
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40 20 1962). The annual mean for Lake Geneva was taken from the CIPEL (International Commission for
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42 21 the Protection of Lake Geneva) reports, and was calculated over the entire water column (Lazzaroto
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44 22 et al., 2005).

45 23 **Statistical analysis** –Temporal maps were used to represent the seasonal patterns of
46
47 24 cladoceran abundance. These maps were created using MatLab software (The MathWorks Inc.
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49 25 Version 7.4.0) by interpolating values between two successive sampling dates. This representation
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51 26 gave an overview of the annual and inter-annual patterns of the abundances of each species. To
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53 27 identify the annual pattern of zooplankton succession, and to evaluate any deviations from this
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55 28 pattern, we used the multivariate method, STATIS. This allows the annual fluctuations of the
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57 29 different species to be synthesized into average annual patterns of species successions that can be
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59 30 compared to one another. Briefly, STATIS is an ordination method designed to analyze several
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61 31 subsets of quantitative data simultaneously. The method can be used to identify the common
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63 32 structure, “the compromise”, shared by the subsets. A detailed description of the mathematical
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65 33 formulation can be found in Escoufier (1973) and Lavit et al. (1994). This method has proved useful

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3 1 in aquatic sciences for the spatial and temporal analysis of plankton (see Licandro and Ibanez, 2000;
4 Anneville et al., 2002b) and fish communities (Gaertner et al., 1998).

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6 3 In this study, the multivariate statistical analyses were run using ADE-4 free software
7 (Thioulouse et al., 1997). STATIS was run on a multi-table data set, which is represented by a
8 matrix containing the sampling dates, as objects, and the 5 zooplankton taxon groups, as variables.
9 Taxon abundances were expressed as logarithms ($\log(x+1)$) in order to diminish variations of
10 cladoceran abundances. A total number of 156 and 113 samples for Lake Geneva and Annecy
11 respectively, were taken into consideration in the analysis. Sampling dates were organized into
12 subsets, each corresponding to a "Lake dataset/Year". The matrix was therefore subdivided into 16
13 subsets Lake/Year (2 lakes x 8 years). This means that looking for the compromise was equivalent
14 to looking for common temporal trajectories between successive years in both lakes. Overall, the
15 method provided information about the similarity between the annual trajectories, the pattern of the
16 common annual trajectory, and the inter-year variability of the annual trajectories of cladoceran
17 communities. Tests for detecting departures from normality (Shapiro-Wilk W -statistic), Pearson
18 correlation and Mann-Whitney Wilcoxon tests for sample comparisons were performed with S-
19 PLUS version 6.1 (Insightful Corp., Seattle, Washington, USA).
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37 20 **Results**

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39 21 *Environmental characteristics of the lakes and specific features of 2003:* In winter, the average
40 temperatures measured in the first 10 meters of the two lakes were similar. Differences between the
41 temperatures in the two lakes began in April, and became significant (Wilcoxon test, p -value <0.05)
42 in May. From May to August, Lake Annecy was on average 2 °C warmer than Lake Geneva. In
43 September, the temperature decreased in both lakes, and the differences between them were no
44 longer statistically significant. In contrast, average temperatures measured in the first 50m of water
45 followed differing patterns. According to these average values, Lake Geneva was warmer except
46 from April to July when the temperatures were not significantly (Wilcoxon test, p -value >0.05)
47 different from those recorded in Lake Annecy.
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55 30 In 2003, from June to August, the temperatures measured in the upper 10 meters were
56 higher than usual in both lakes (Fig. 1). In Lake Geneva, the water temperatures rose only in the 0-
57 10m layer while extremely high air temperatures were recorded during the summer of 2003. Over
58 the whole 0-50m layer, lower than usual average water temperatures were actually recorded (Fig.
59 1), indicating marked stratification within this layer.
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3 1 Lakes Geneva and Annecy have very different total phosphorus contents. The annual
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5 2 averages of the total phosphorus concentrations were around $38 \mu\text{P.L}^{-1}$ in Lake Geneva, versus
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7 3 $6 \mu\text{P.L}^{-1}$ in Lake Annecy. There were also differences between these two lakes with regard to their
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9 4 phytoplankton communities. Significant differences in the total abundance of phytoplankton were
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11 5 observed from May to August. Phytoplankton was more abundant in Lake Geneva except in May.
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13 6 In Lake Geneva, the average proportion of nanophytoplankton was high in spring (on average 55%
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15 7 from March to May); this dropped to 20% in June, and then remained below 20% throughout the
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17 8 summer (Fig. 1). However, during the exceptional year 2003, the contribution of
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19 9 nanophytoplankton to the total phytoplankton biomass was higher than usual in summer (Fig. 1). In
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21 10 Lake Annecy, nanophytoplankton species make up on average 56% of the total phytoplankton
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23 11 biomass and were dominant throughout the year (Fig. 1). The absolute nanophytoplankton
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25 12 abundances were normally higher in Lake Annecy than in Lake Geneva in summer (Fig. 1), but
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27 13 during 2003, nanophytoplankton was exceptionally more abundant than usual in July in Lake
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29 14 Geneva and in August in Lake Annecy.

30 16 **Annual dynamics of cladocera:** The cladoceran taxa analyzed accounted for 98% and 77% of
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32 17 the total cladoceran abundance in Lakes Geneva and Annecy, respectively. Temporal maps of their
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34 18 abundance in successive years revealed seasonal patterns (Fig. 2), which remain fairly stable for
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36 19 some taxa, but which differ in the two lakes. In Lake Geneva, the abundance of *Daphnia* peaked in
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38 20 May, and then decreased. In Lake Annecy, in contrast, the population peak occurred in June and
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40 21 persisted till September. Higher abundances of *Eubosmina* were recorded in the spring in Lake
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42 22 Geneva, whereas they occurred in late summer or autumn in Lake Annecy. The cladoceran
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44 23 predators *Leptodora* and *Bythotrephes* were less abundant in Lake Annecy than Lake Geneva, their
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46 24 abundances being significantly different in the two lakes from May to August (Wilcoxon test, p-
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48 25 value<0.005). The seasonal population pattern of *Leptodora* was similar in the two lakes, with a
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50 26 maximum during July and August. The peak levels of *Bythotrephes* were reached in June in Lake
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52 27 Geneva, whereas in Lake Annecy the highest biomass for this species was recorded from the end of
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54 28 summer till December.

55 30 **Identification of the compromise model:** STATIS indicates that cladocerans were mostly
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57 31 absent during winter in both lakes. In Lakes Geneva and Annecy, summer was mainly characterized
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59 32 by *D. galeata/hyalina* and the large carnivorous species *Leptodora* – *Bythotrephes*, which follow on
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33 from the spring species, such as *Eubosmina* - *D. longispina* (Fig. 3). The contributions of the
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different species to this model were expressed as the correlations between species abundance and

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3 1 the factorial coordinates (Table II). All the species contributed to the formation of axis I, the main
4 contributor being *D. galeata/hyalina* (Pearson, t-test, p-value<0.01). Axis II separates the species
5 2 that predominate in spring (“*Eubosmina - D. longispina*”) from those that predominate in summer
6 3 (“*Leptodora – Bythotrephes*”) (Pearson, t-test, p-value<0.05).
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9 5 All the subsets “Lake/Year” made a strong and homogenous contribution to this annual
10 6 pattern (Table III). However, the scores on the second eigenvector of the Euclidean space indicated
11 7 a segregation between the lakes (Table III). They indicated differences in the annual succession
12 8 pattern of zooplankton in the two lakes, and suggested that there were two main alternative annual
13 9 patterns, each of which was characteristic of one of the lakes. However, in 2003, the annual pattern
14 10 recorded in both lakes resembled the one usually reported for Lake Annecy.
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17 13 ***Analysis of the variability in the annual trajectories:*** Individual projections of the samples
18 14 for the successive subsets “Lake/Year” on the plane of the compromise confirm inter-lake
19 15 differences in the seasonal patterns of cladoceran communities. Compromises for Lake Geneva and
20 16 Lake Annecy were represented separately on Axis I and II (Fig. 4A-C)). Comparing the distribution
21 17 of the samples along axes I and II allowed us to interpret differences between the seasonal patterns
22 18 of taxa succession in the two lakes.
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25 21 On axis I, the scores of the Lake Geneva samples became negative in May, one month earlier
26 22 than those of Lake Annecy (Fig. 4A). This indicated that the spring increase in cladoceran
27 23 abundances occurred earlier and was more pronounced in Lake Geneva than in Lake Annecy (Fig
28 24 4B).
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30 26 Axis II separated the dates characterized by high abundances of *Eubosmina* or *D. longispina*
31 27 from those with low abundances of these species combined with high abundances of the
32 28 carnivorous *Leptodora* or *Bythotrephes*, which were characteristic of the summer community (Fig.
33 29 3). In Lake Geneva, *Eubosmina* or *D. longispina* were abundant until June, with maximum
34 30 abundances recorded in May (Fig. 4D). In July, the scores for the samples switched to positive
35 31 values (Fig. 4C), indicating a change towards low abundances of *Eubosmina* or *D. longispina*, and
36 32 high abundances of *Leptodora* or *Bythotrephes* (Fig. 4D). In Lake Annecy, the scores of the
37 33 samples became positive in May, and reverted to negative values in September (Fig. 4C). The
38 34 summer community was therefore observed on average two months earlier than in Lake Geneva,
39 but this was not maintained for long. Furthermore, maximum abundances of *Eubosmina* or *D.*
40 *longispina* were not restricted to the spring season, as was the case in Lake Geneva. Indeed, after a
41 slight dip in July, their abundance subsequently began to increase again, to peak in September (Fig.
42 4D).
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Variability in the timing of the transition between seasonal communities was strongly linked to water-temperature. As can be seen in Fig.3, differences between the growth period and the period of low plankton activity were highlighted on axis I. The start of cladoceran growth can thus be assigned to the first date when scores become positive on axis I. As we have already pointed out, spring zooplankton growth usually started earlier in Lake Geneva, with a difference of 22 to 70 days observed between the two lakes. The amplitude of the inter-annual fluctuations in the timing of the beginning of cladoceran growth was around one month in Lake Geneva, and two months in Lake Annecy. For both lakes, the date of zooplankton development was correlated with April water-temperatures measured within the 0-50m depth layer (Pearson, t-test, p-value<0.05). These temperatures were also significantly correlated with winter air temperatures (Pearson, t-test, p-value<0.05) and significant correlation (Pearson, t-test, p-value<0.05) between date of zooplankton development and winter air temperatures was recorded in Lake Geneva. The switch to a summer community was taken to occur on the date when the scores on axis II became positive. These dates displayed marked inter-annual variability, but no significant correlation with water-temperature (Pearson, t-test, p-value>0.05).

In 2003, the pattern observed in Lake Geneva (Fig. 5) fitted the usual model for Lake Geneva along axis I ($R^2=0.94$, p-value<0.001), but not along axis II ($R^2=0.001$; p-value=0.93). Residuals from the model were highest in August and September, when the score along axis II became negative, indicating an increase in *Eubosmina* or *D. longispina* and a decrease in *Leptodora* or *Bythotrephes* (Fig. 4D). Abundances of *Eubosmina* were indeed higher than usual (Fig. 6). In contrast, *Leptodora* and *Bythotrephes* were less abundant in August and September in 2003 than in the other years (Fig. 6). Water temperature (T0-10) and water stratification were the main environmental parameters that distinguished the year 2003 (Fig. 7), higher values than usual being recorded for both.

Discussion

We have investigated the seasonal variability in zooplankton composition in Lakes Geneva and Annecy, and identified differences in zooplankton responses in these two neighbouring lakes when exposed to the same exceptional heat wave in 2003.

The usual overall seasonal pattern identified in both lakes by the method STATIS was characterized by low cladoceran densities in winter. The population of cladoceran herbivores increased and then decreased in parallel with the abundance of nanophytoplankton species. The decline in abundance was probably mainly induced by food-limitation and fish predation as

1 suggested by the PEG model (Sommer et al., 1986), and according to Gawler et al. (1988) by
2 predation by carnivorous cladocerans (i.e. *Leptodora* and *Bythotrephes*), which reach their greatest
3 abundance at the end of spring and in summer.

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5 *Lake specificity:* The seasonal pattern exhibited by cladocerans varies in their timing of
6 development as well as in the pattern of taxon succession in summer, in the two lakes. It has been
7 shown that the rate of spring zooplankton development depends on the trophic state of the lake, and
8 is generally slower in oligotrophic lakes than in eutrophic lakes (Sommer et al., 1986). Accordingly,
9 the development of cladocerans usually started earlier in Lake Geneva (eutrophic-mesotrophic) than
10 in Lake Annecy (oligotrophic). The divergence in the timing of cladoceran development may also
11 be attributable to discrepancies in the dynamics of the water column warming. For instance, despite
12 the greater vernal increase of warmer temperatures in the upper 10m in Lake Annecy, the average
13 temperatures within the 0-50m layer were usually higher in Lake Geneva until April. Temperature
14 modulates the duration of egg development and this, together with the availability of food, can
15 control the abundance of zooplankton in winter and spring (Saunders et al., 1999). The differences
16 in late-winter and early spring water temperatures could also affect the rate of development of the
17 cladocerans in spring, as revealed by the inter-annual variability in *Daphnia* in other European lakes
18 (Straile et al., 2003).

19 In Lake Geneva, spring was characterized by a rapid increase in herbivorous cladocerans, the
20 subsequent increase in grazing pressure coincided with the decline of the spring phytoplankton
21 community which was dominated by small edible algae, as shown in Figure 1. The phytoplankton
22 community then changed into a community dominated by large algae (Anneville et al., 2002a,b),
23 resulting in low filtration efficiency. As a result of the effects of temperature-influenced clearance
24 rates, the interference-capability, the herbivorous species then decline to reach low levels in winter
25 (Sommer et al., 1986). In contrast, in Lake Annecy, the continued high proportion of
26 nanophytoplankton in the total phytoplankton biomass throughout the summer might favour
27 herbivorous species and could explain the presence of *Eubosmina* and *D. longispina* during this
28 season. Differences in the abundance of herbivorous cladoceran species during the summer in Lake
29 Annecy and in Lake Geneva were therefore probably attributable to the seasonal dynamics of
30 phytoplankton, which in turn have been linked to the trophic-state of the lakes (Sommer et al.,
31 1986). Furthermore, invertebrate predators are recognized regulators of the succession of smaller
32 herbivorous species (Sommer et al., 1986; Manca et al., 2000; Chang and Hanazato, 2003; Uusitalo
33 et al., 2003). In Lake Geneva, the growth of the large, thermophilic raptorial zooplankton
34 *Leptodora* and *Bythotrephes*, is known to control the densities of herbivorous species (Gawler et al.,

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3 1 1988), and consequently explained the limited abundance of herbivorous species during the summer
4 2 season. In contrast, in Lake Annecy the high density of zooplanktivorous fish (i.e. perch and
5 3 whitefish) exerted high predation pressure on *Leptodora* and *Bythotrephes* (Palmer et al., 2001;
6 4 Gerdeaux et al., 2002; Uusitalo et al., 2003), and this might control the abundance of these large
7 5 predaceous cladocerans in summer, as suggested by the low abundance of *Leptodora* and
8 6 *Bythotrephes* in Lake Annecy. The predation pressure they exerted on herbivorous zooplankton was
9 7 therefore probably lower in Lake Annecy and so may not prevent the occurrence of small
10 8 herbivorous species during the summer. Bottom-up and top-down control may both be responsible
11 9 for the differences between the two Lakes with regard to the seasonal succession of cladoceran
12 10 species.

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23 12 *Inter-annual changes in the seasonal dynamics of cladoceran communities and impact of the heat-*
24 13 *wave 2003:*

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26 14 We have shown that the variations in the seasonal pattern in different years take two main
27 15 forms. The first concerned the timing of cladoceran development and the presence of carnivorous
28 16 invertebrates. The second concerned the taxon succession pattern in summer. The timing of the
29 17 herbivorous peak varied according to temperature, and this confirmed the findings of earlier studies
30 18 run over a longer time-span that have shown that temperature controls phenology and synchronous
31 19 annual events in different lakes (Straile, 2002). The development of zooplankton in the spring
32 20 occurred on average approximately two weeks earlier in Lake Geneva, and has been in phase with
33 21 the North Atlantic Oscillation for the last 30-years (Anneville et al., 2002a). In lakes Geneva and
34 22 Annecy, the variability of water temperature was not enough to explain the fluctuation in the timing
35 23 of occurrence of *Leptodora-Bythotrephes* and the decline of *Eubosmina* and *D. longispina*.
36 24 However, higher biomass at temperatures above 15 °C and a positive correlation between water
37 25 temperature and *Leptodora* abundance have been recorded elsewhere (Herzig, 1995). It is thus
38 26 plausible that other parameters, such as food abundance or predation by fish, superimposed over the
39 27 effects of temperature, might actually have more influence in determining the timing of these
40 28 carnivorous groups during the years studied.

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53 29 The results showed 2003 to be an exceptional year for the cladoceran succession pattern in
54 30 Lake Geneva, but not in Lake Annecy. The pattern in 2003 was driven by marked changes in water
55 31 temperatures that were supposed to be the main cause of deviations from the usual seasonal
56 32 patterns. In both lakes, the surface layer (0-10m) appeared to be markedly affected by this major
57 33 heat wave, leading to increased stratification as predicted by models (Jankowski et al., 2006). In
58 34 Lake Geneva, surface water temperatures reached exceptionally high values in spring, which could

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3 1 explain the earlier than usual development of the carnivorous cladocerans (*Leptodora* and
4 2 *Bythotrephes*) in June. After this, increased stratification most probably affected vertical nutrient
5 3 profiles and the regeneration of the eutrophic layer in late-spring and summer. We speculate that
6 4 this has affected phytoplankton development and composition, as suggested by the fact that the
7 5 summer biomass was lower than in the previous years (Druart et al., 2004) despite higher than usual
8 6 abundances of nanophytoplankton. The marked stratification, together with a higher percentage of
9 7 nanophytoplankton, led to unusual environmental conditions in summer that were similar to those
10 8 observed in Lake Annecy. Probably related to this, unusual high abundances of *Eubosmina* in Lake
11 9 Geneva were observed in summer, and resulted in an annual pattern quite similar to that usually
12 10 observed in Lake Annecy.
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21 11 Many studies have shown the synchrony between climate and plankton. Some of them
22 12 underline spatial coherence in the response of plankton (Straile, 2002). The results presented here
23 13 suggest that for extreme conditions which are likely to become more frequent in the second half of
24 14 this century (IPCC, 2007), there is no coherence and therefore the response of plankton to extreme
25 15 climatic events may be unpredictable.
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30 16 In conclusion, we have shown that the timing of the spring development of cladocerans is
31 17 sensitive to the late-winter water temperature, and can therefore be indicative of climate change. In
32 18 contrast, the consequences of inter-annual meteorological variability and extreme events on the
33 19 seasonal pattern of cladoceran communities were not the same in both lakes. This may be
34 20 attributable to their morphometry that results in subtle differences in their hydrodynamic properties
35 21 and thus dynamics of thermal stratification (intensity and duration). The differences found in the
36 22 lakes' responses may also be due to differences in food web structures i.e. predator abundance and
37 23 phytoplankton species involved in the seasonal succession, which are in turn strongly influenced by
38 24 the trophic status of the lake. This means that, the consequences of physical forcing on the
39 25 phenology of similar zooplankton taxa, located in the same region with similar weather conditions,
40 26 can differ depending on the biotic properties or hydrodynamics of the lakes concerned.
41 27 Superimposed over the large scale forcing factors, the local variability can lead to different effects
42 28 on the thermal structure of the water column in lakes, and consequently on the seasonal pattern of
43 29 phytoplankton, and the rate of development of zooplankton. Consequently, by highlighting the
44 30 complexity of the relationships between climate and freshwater ecosystems, and by cautioning
45 31 regarding the extrapolation of ecological responses to climate, these findings contribute to the
46 32 debate on the predictability of climate change impacts on aquatic ecosystems.
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Acknowledgments

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Table and Figure legends

Table I. Morphological and trophic properties of the lakes studied.

Table II. Correlation between species abundance (*D.long*: *D. longispina*, *D. gal/hy*: *D. galeata* and *D. hyalina*, *E.lo/mi*: *Eubosmina*, *Lepto*: *Leptodora*, *Bytho*: *Bythotrephes*.) and factorial coordinates on the two first axes. ** and * indicate that correlation is significant at $p < 0.01$ and 0.05 respectively.

Table III. Description of the annual structure defined for each subset “Lake/Year”, which are named by a letter (A or G) and a number. The G stands for Lake Geneva and the A for Lake Annecy, the number indicates the year. The Weight: contribution of each subset in the construction of the compromise. Cos^2 : fit of each subset to the compromise. Axis II: Scores on the second eigenvector on the Euclidean space showing the similarities between the subsets “Lake/Year”.

Fig.1. Box-plot representing the seasonal pattern of : water-temperature in the 0-10m layer, water-temperature in the 0-50m layer, contribution of nanophytoplankton (%) to the total abundance of phytoplankton, abundance of nanophytoplankton ($\log+1$). • indicate the values recorded in 2003. The horizontal line in the box is the median, the bottom and the top of the box correspond to the first and third quartiles respectively. The “whiskers” are drawn to the nearest value not beyond a standard span from the quartiles which is $1.5 * (\text{Inter-quartile Range})$.

Fig. 2. Temporal maps showing the seasonal patterns and inter-annual changes in the abundance of the different cladoceran groups considered in Lakes Geneva (a: *D. longispina*, b: *D. galeata* and *D. hyalina*, c: *Eubosmina*, d: *Leptodora*, e: *Bythotrephes*) and Annecy (f: *D. longispina*, g: *D. galeata* and *D. hyalina*, h: *Eubosmina*, i: *Leptodora*, j: *Bythotrephes*).

Fig. 3. Compromise for both lakes: A) Projection of all the samples (dots) and barycentres of the months on the space of axes I-II. Barycentres of months are represented by numbers from 1 (for January) to 12 (for December). B) The contribution of the taxa to the formation of the axes is represented by their projection in the corresponding plane of the compromise: *Lepto*: *Leptodora*,

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1 Bytho: *Bythotrephes*, *D. gal/hy*: *D. galeata* and *D. hyalina*, *D.long*: *D. longispina*, *E.lo/mi*:
2 *Eubosmina*.

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4 **Fig. 4.** A-C: Box-plot describing the annual patterns of the cladoceran community observed in
5 Lakes Geneva and Annecy on axis I (A) and II (C) of the compromise. The main species
6 contributing to the formation of the axis (*D. gal/hy*: *D. galeata* and *D. hyalina*, *Lepto*: *Leptodora*,
7 *Bytho*: *Bythotrephes*, *D.long*: *D. longispina*, *E.lo/mi*: *Eubosmina*.) are specified for each axis
8 respectively. The dot through the box is the median, the bottom and the top of the box correspond to
9 the first and third quartiles respectively. The “whiskers” are drawn to the nearest value not beyond a
10 standard span from the quartiles which is $1.5 \times (\text{Inter-quartile Range})$. B-D: Annual dynamics of the
11 abundance of the cladoceran species that contribute to the formation of axis I (B) and axis II (D).

12
13 **Fig. 5.** Comparison of the exceptional year 2003 and the usual annual patterns of cladoceran
14 succession observed in Lake Geneva.

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16 **Fig.6.** Abundance ($\log+1$) of *Eubosmina*, *D. longispina*, *Leptodora* and *Bythotrephes* during August
17 and September in 2003 (\blacktriangle) compared to the other years (box-plot) in Lake Geneva. The dot
18 through the box is the median, the bottom and the top of the box correspond to the first and third
19 quartiles respectively. The “whiskers” are drawn to the nearest value not beyond a standard span
20 from the quartiles which is $1.5 \times (\text{Inter-quartile Range})$.

21
22 **Fig. 7.** Normalized values of summer averages (May to September) of environmental parameters
23 observed from 1995 to 2002 (box-plot), and in 2003 (\blacktriangle) in Lake Geneva. The dot through the box
24 is the median, the bottom and the top of the box correspond to the first and third quartiles
25 respectively. The “whiskers” are drawn to the nearest value not beyond a standard span from the
26 quartiles which is $1.5 \times (\text{Inter-quartile Range})$. Nano: abundance in nanophytoplankton, Nano%:
27 contribution of nanophytoplankton (%) to the total abundance of phytoplankton, Carn: abundance
28 of carnivorous cladocerans, T0-50: water-temperature in the 0-50m layer, T0-10: water-temperature
29 in the 0-10m layer, Strat: Index of stratification.

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3 **1 Table I.**
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	Lake Geneva	Lake Annecy
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3 **Table II**
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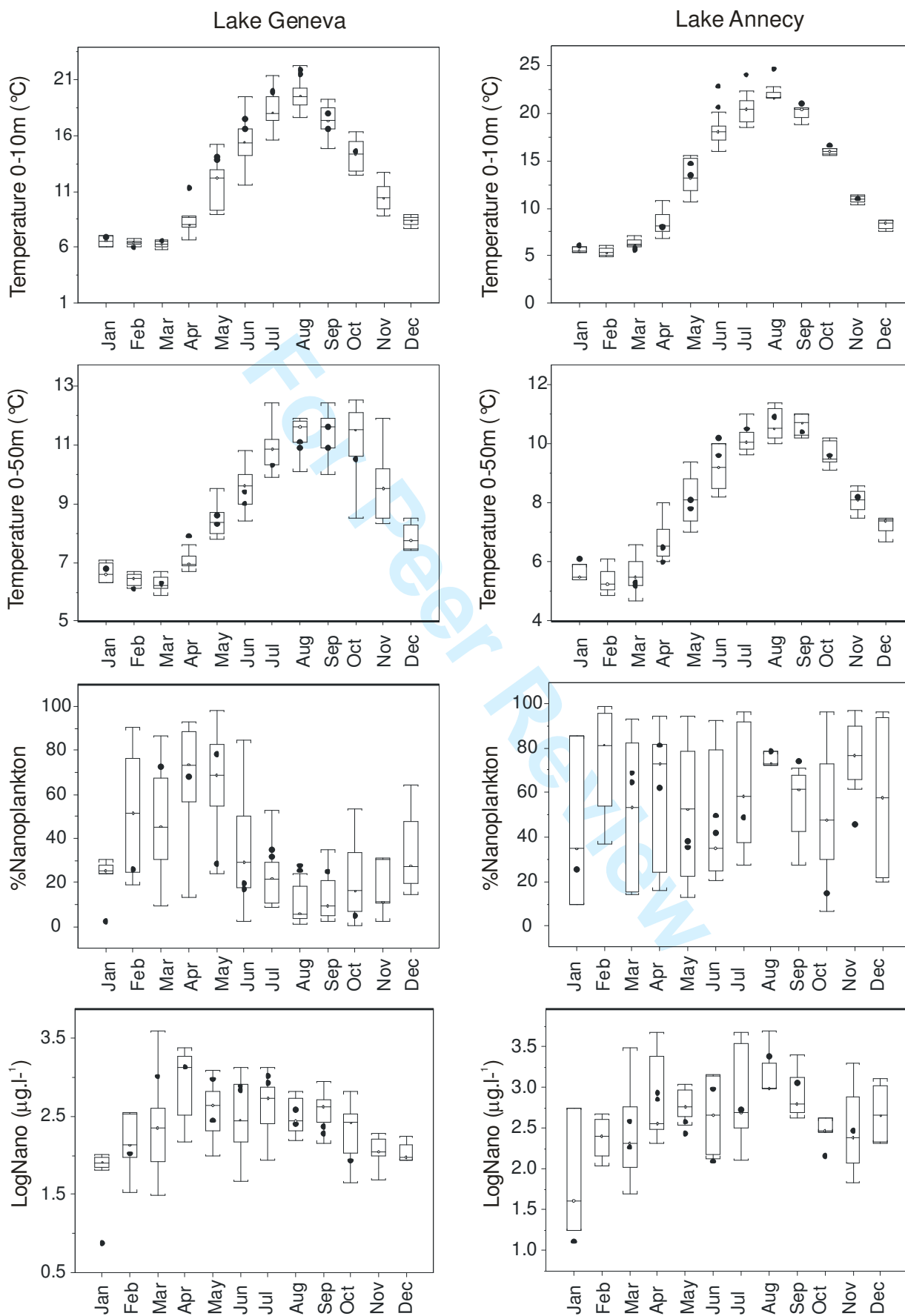
	Abrev.	Axis I	Axis II
10 <i>D longispina</i>	D.long	-0.39 **	-0.30 **
11 <i>D galeata & D hyalina</i>	D.gal/hy	-0.82 **	0.03
12 <i>E longispina & E mixta</i>	E.lo/mi	-0.22 **	-0.66 **
13 <i>Leptodora</i>	Lepto	-0.71 **	0.36 **
14 <i>Bythotrephes</i>	Bytho	-0.50 **	0.14 *

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3 **Table III**
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Subsets	Lakes	Years	Weights	Cos2	AxisII
G95	Geneva	1995	0.27	0.94	0.021
G96	Geneva	1996	0.26	0.86	0.162
G97	Geneva	1997	0.25	0.81	0.331
G98	Geneva	1998	0.24	0.70	0.231
G99	Geneva	1999	0.25	0.75	0.373
G00	Geneva	2000	0.27	0.94	0.016
G02	Geneva	2002	0.26	0.83	0.046
G03	Geneva	2003	0.23	0.63	-0.405
A95	Annecy	1995	0.25	0.80	-0.117
A96	Annecy	1996	0.26	0.83	-0.160
A97	Annecy	1997	0.26	0.84	-0.041
A98	Annecy	1998	0.22	0.60	0.384
A99	Annecy	1999	0.23	0.58	0.006
A00	Annecy	2000	0.26	0.84	-0.008
A02	Annecy	2002	0.24	0.76	-0.341
A03	Annecy	2003	0.23	0.66	-0.524

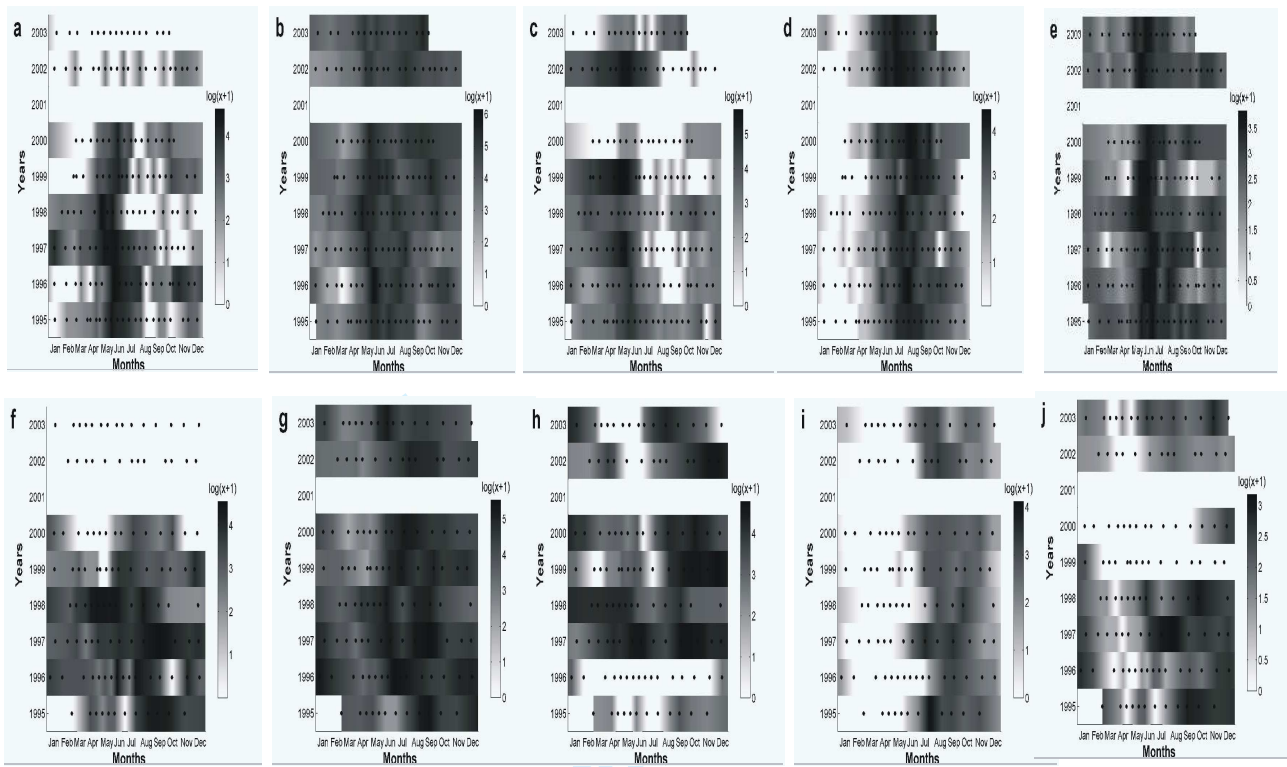
1 O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 1**



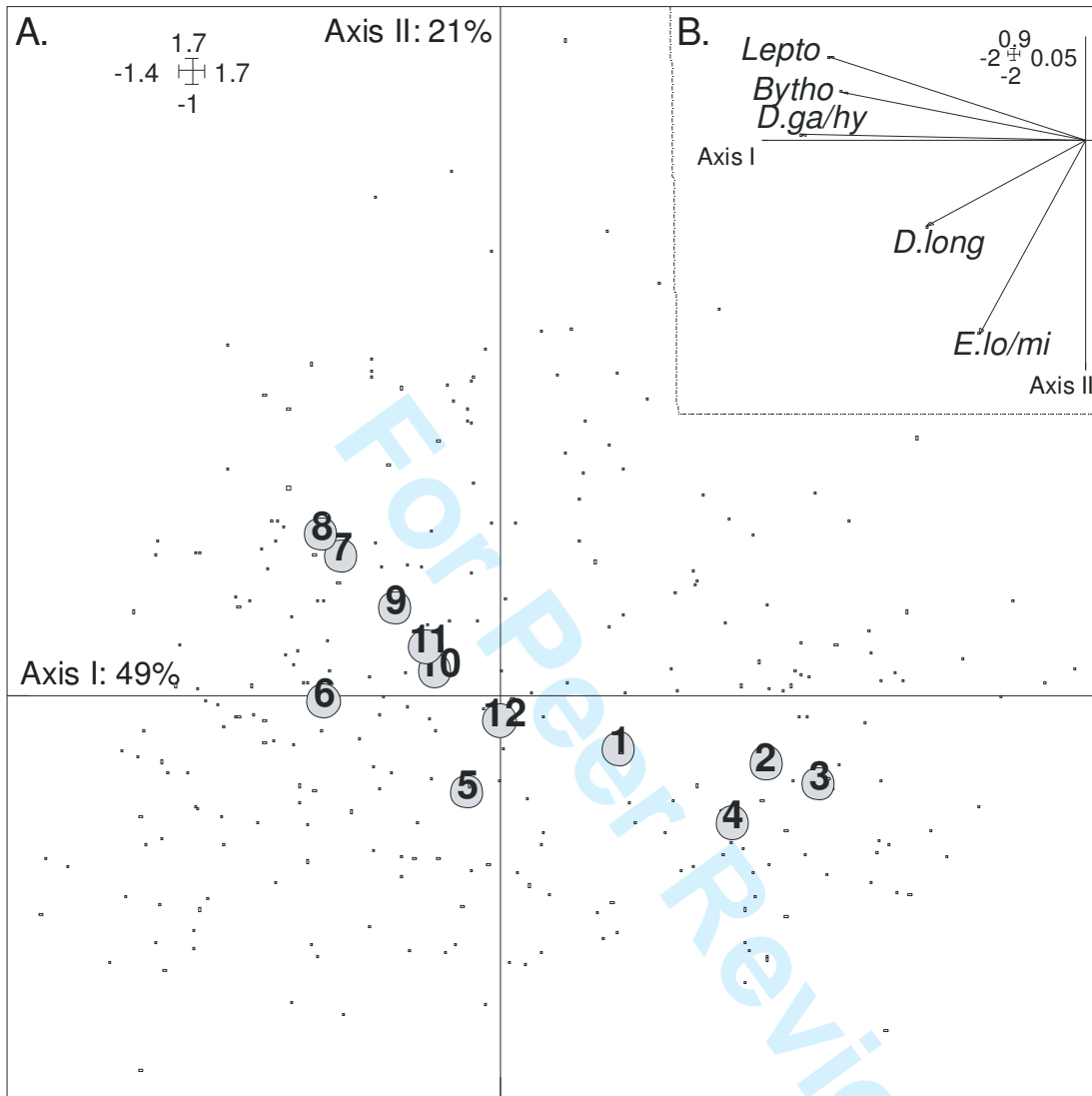
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1 O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 2**

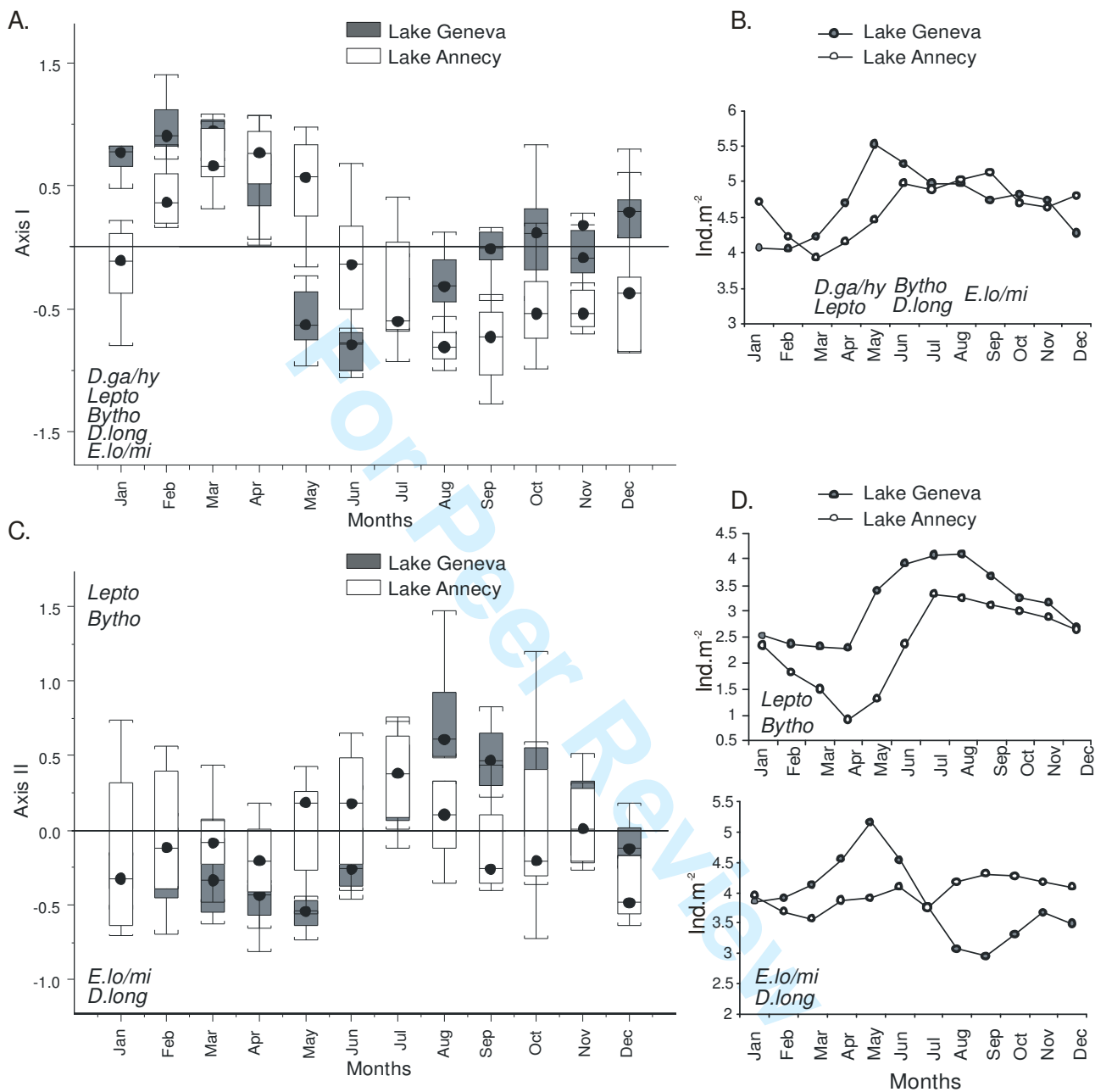


O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 3**



1 O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 4**

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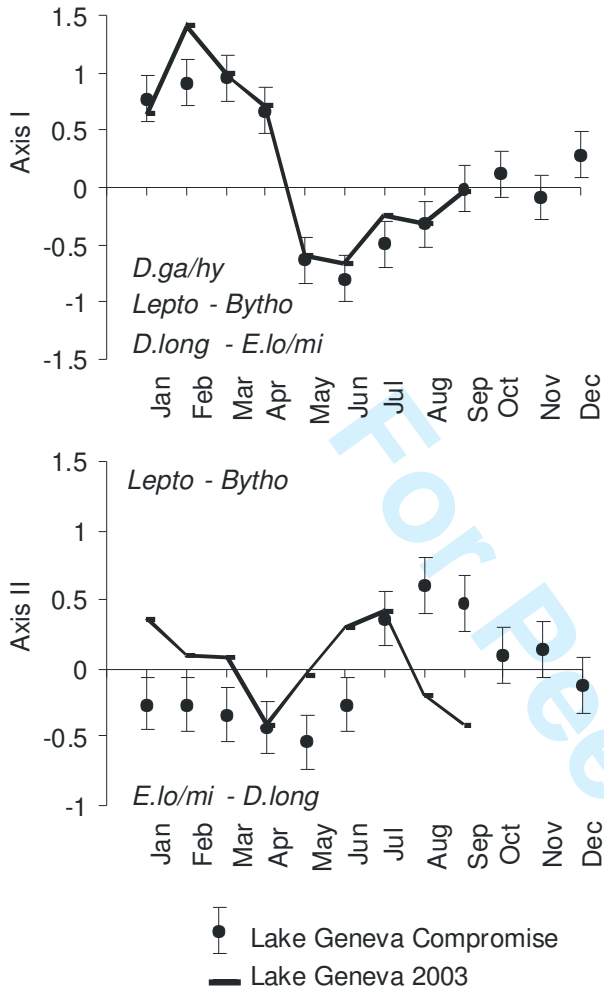
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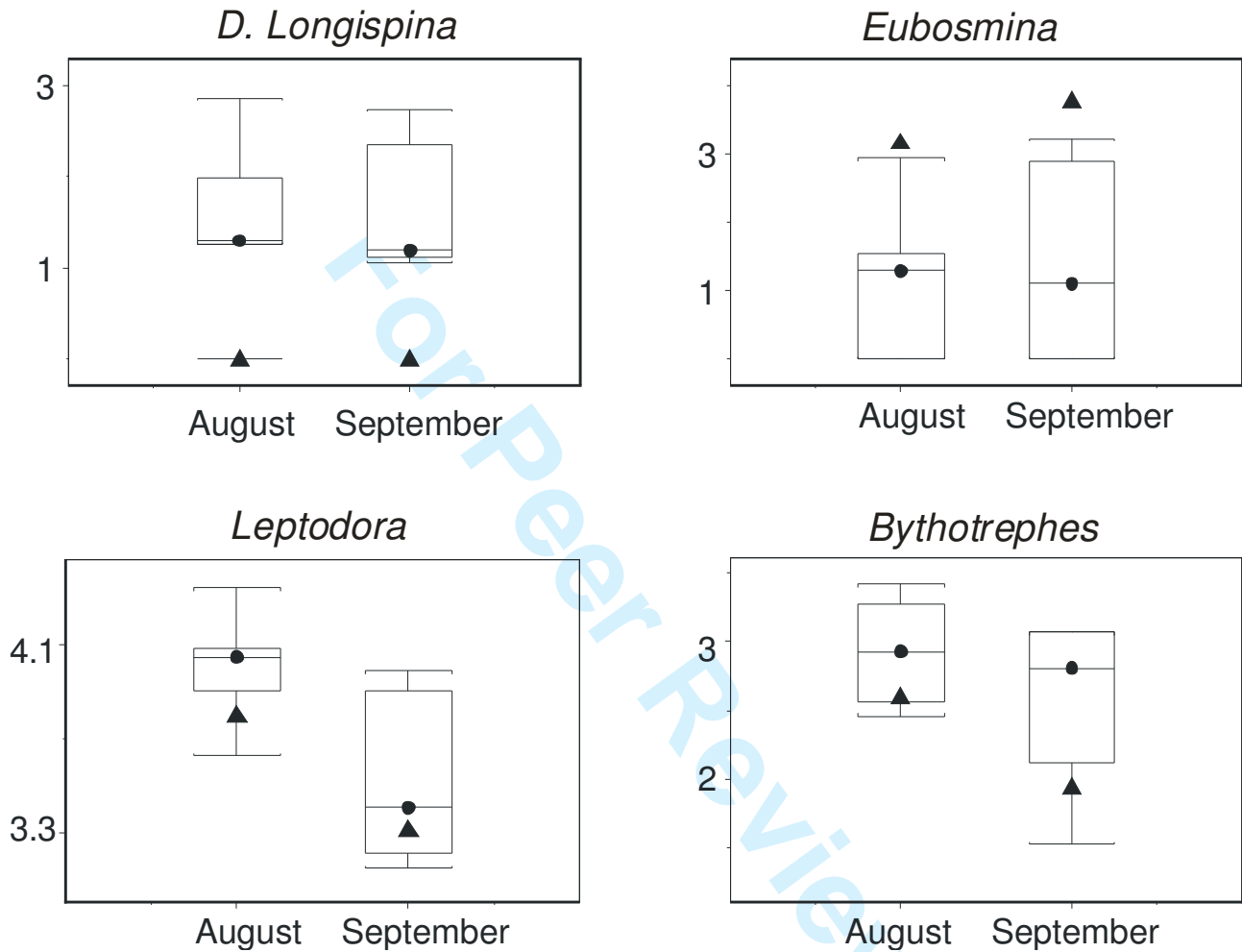
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O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 5**



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3 1 O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 6**
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O. Anneville, J. C. Molinero, S. Souissi and D. Gerdeaux - **Figure 7**

