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Local forcings affect lake zooplankton vulnerability and response to climate warming

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Abstract. While considerable insights on the ecological consequences of climate change have been gained from studies conducted on remote lakes, little has been done on lakes under direct human exposure. Ecosystem vulnerability and responses to climate warming might yet largely depend on the ecological state and thus on local anthropogenic pressures. We tested this hypothesis through a paleolimnological approach on three temperate large lakes submitted to rather similar climate warming but varying intensities of analogous local forcings (changes in nutrient inputs and fisheries management practices). Changes in the structure of the cladoceran community were considered as revealing for alterations, over the time, of the pelagic food web. Trajectories of the cladoceran communities were compared among the three study lakes (Lakes Geneva, Bourget, and Annecy) over the last 70–150 years. Generalized additive models were used to develop a hierarchical understanding of the respective roles of local stressors and climate warming in structuring cladoceran communities. The cladoceran communities were not equally affected by climate warming between lakes. In Lake Annecy, which is the most nutrient-limited, the cladoceran community was essentially controlled by local stressors, with very limited impact of climate. In contrast, the more nutrient-loaded Lakes Geneva and Bourget were more sensitive to climate warming, although the magnitude of their responses and the pathways under which climate warming affected the communities varied between the two lakes. Finally, our results demonstrated that lake vulnerability and responses to climate warming are modulated by lake trophic status but can also be altered by fisheries management practices through changes in fish predation pressure.

Key words: climate change; food web; human stressors; lake; paleolimnology; time series modeling.

INTRODUCTION

While climate change is increasingly acknowledged as an important driver of lake ecosystems (George and Harris 1985, Adrian et al. 1995, IPCC 2001), our understanding of the mechanisms by which climate affects lakes is still patchy (Keller 2007). The complexity of the issue of lake responses to climate change arises from the fact that the various climatic components act on lake physical, chemical, and biological characteristics through many interconnected pathways (Battarbee 2000, Leavitt et al. 2009). In addition, the relative importance and potential interactions of these different pathways may vary, depending on the nature and magnitude of climate variability, but also according to lake characteristics (Pham et al. 2008, Cardille et al. 2009). Understanding and potentially forecasting the impact of climate variability on lakes therefore require that we order and scale up these different pathways (Leavitt et al. 2009). Achieving this objective requires

long-term data sets that can be obtained using paleolimnological records spanning time ranges long enough to encompass pre- and post-disturbance periods (Battarbee 2000).

Much effort has been dedicated to reconstructing past changes in polar and alpine lakes over the last century (e.g., Battarbee et al. 2002, Quinlan et al. 2005, Smol et al. 2005) since (1) they are highly climate sensitive (ACIA 2004) and (2) their remoteness allows us to obtain a signal of their response to climate change that is not obscured by noise from local human influences (Battarbee et al. 2002). These studies have considerably improved our understanding of the ecological consequences of climate change on this specific category of lakes. Yet, the geographical nonuniformity in climate changes (which depend on the latitude, longitude, and altitude [Blenckner and Hillebrand 2002, Livingstone et al. 2005]) may limit the generalization of such observations to other climatic regions.

The impact of climate variability on temperate lakes has been much less investigated and most of the knowledge has been provided by the study of long-term data series, hence restricting the implications of these results to the few lakes that have been subjected to long-

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term monitoring. Although the impacts of climate change are expected to be less severe in temperate than in polar or alpine regions (ACIA 2004), most of these studies provided strong evidences of climate-related trends in physical, chemical, or biological components of temperate lakes (e.g., DeStasio et al. 1996, Straile et al. 2003, Winder and Schindler 2004). Their trajectories, facing global changes, may also be complicated by interactions between climate and local stressors, since the combination of concomitant environmental forcings can amplify or hide their individual effects on the studied ecosystem (e.g., Matzinger et al. 2007, Pham et al. 2008). Surprisingly, paleolimnological records of the recent ecological trajectory of temperate lakes are still quite rare and very few have attempted to unravel or hierarchize the impact of various external forcings (e.g., Simpson and Anderson 2009, Bennion et al. 2012, Dong et al. 2012).

The purpose of this work was to compare, over the last century, the responses of the zooplankton community of three temperate, large, and deep peri-alpine lakes submitted to rather similar climate variability, but with varying intensities of analogous local forcings (changes in nutrient inputs and fisheries management practices). The overarching aim was to hierarchize the role of local pressures vs. climate warming on the responses of zooplankton over the past century. Our working assumption was that the zooplankton communities of these three lakes should show similar responses to climate warming, consistently with Straile and Adrian's (2000) findings. The alternative hypothesis was that, because these lakes have been under different anthropogenic local forcings, their response to climate warming should be distinct (Umbanhowar et al. 2011). For such purposes, long-term changes in the cladoceran community structure were reconstructed from their sub-fossil remains in all three lakes, using a paleolimnological approach. This study focused on cladocerans, rather than on other paleo-proxies, since they are highly sensitive and react quickly to all three considered local and global forcings (lake nutrient levels, fisheries management practices, and climate). Indeed, zooplankton, and cladocerans in particular, respond to changes in nutrient levels, which modify the quantity and quality of their food resources (Reynolds 1998) through a bottom-up effect (McQueen et al. 1986). In addition, changes in fish community and, potentially, in the nature and magnitude of size-selective predation may induce changes in the size structure of cladoceran prey community by top-down effects (Brooks and Dodson 1965). Finally, climate warming may affect cladoceran community, directly through its influence on biological processes (Moore et al. 1996) and indirectly since species-specific responses to climate warming may affect the phenological coupling of trophic relationships (Winder and Schindler 2004) leading to cascading effects up or down in the food web (Moore et al. 1996, Jeppensen et al. 2010). Hence, we considered that

temporal alterations in the composition and size structure of the cladoceran community should mirror the impacts of the considered forcings on the pelagic food web.

MATERIAL AND METHODS

Study sites

Lakes Geneva, Bourget, and Annecy are all warm-montic lakes located on the northwest edge of the French Alps. The surface water of these lakes is never frozen over. They are the largest deep lakes in France with surface areas of 582, 42, and 27 km² and maximum depths of 309, 145, and 69 m for Lakes Geneva, Bourget, and Annecy, respectively. The geographical vicinity of these lakes, with Lakes Bourget and Annecy situated within 50 and 70 km of Lake Geneva, places them within a similar climatic context characterized mostly by a global increase in temperature over the last 20 years (Auer et al. 2007). All three lakes are currently submitted to monitoring surveys, started in 1957 for Lake Geneva (managed by the International Commission for the Protection of Lake Geneva Waters and the French National Institute for Agronomical Research–INRA), 1996 for Lake Annecy (managed by the Intercommunal Association of Lake Annecy and INRA), and 2004 for Lake Bourget (managed by the Lake Bourget water agency and INRA).

Supposedly oligotrophic in the late 19th century, Lakes Geneva, Bourget, and Annecy underwent eutrophication in the mid-20th century, due to industrial effluents and domestic sewage (Giguët-Covex et al. 2010, Perga et al. 2010). The magnitude of eutrophication, however, differed between lakes. Lakes Geneva and Bourget reached a eutrophic status by the end of the 1970s while Lake Annecy never got higher than oligo-mesotrophic (Perga et al. 2010). Phosphorus abatement measures have successfully reduced total phosphorus concentrations ([TP]) in the water column of the three lakes over the last 40–30 years. Based on their winter [TP], Lake Annecy is now oligotrophic while the other two are currently oligo-mesotrophic. In addition, fish communities have been modified through fisheries management practices, which are essentially centered on the zooplanktivorous whitefish, *Coregonus lavaretus*. In brief, whitefish stocking is a common practice to support the fishery recruitment (Gerdeaux et al. 2006). It was introduced in Lake Annecy by the end of the 19th century and stocked sporadically from 1900 to the 1930s and then annually from 1936 to 1997. In Lakes Geneva and Bourget, stocking has been performed to support local populations (since 1970 for Lake Geneva and every year during 1943–1965 and 1986–2008 for Lake Bourget [Champigneulle et al. 2001]).

Paleolimnological reconstructions were conducted for Lakes Geneva and Bourget while data for Lake Annecy were available from a previous study (Perga et al. 2010).

Coring and chronology

Several short sediment cores (30–72 cm long) were collected in the lakes' deepest points in May 2010 (Lake Geneva) and February 2009 (Lake Bourget) using a quadruple gravity corer (UWITEC, Mondsee, Austria). Sediment dating was performed from one reference core for each lake using radiometric methods (^{210}Pb , ^{226}Ra , ^{137}Cs , and ^{241}Am activities) and counting of annual laminations, which provided accurate chronologies for high-resolution sampling in both lakes (Appendix A). All working cores (those on which paleolimnological analyses were performed) were sampled following annual laminations, with the same temporal precision (annual or, at most, biennial resolution) and correlated to the reference core using lithological tie points and lamina counting performed on both reference and working cores (Appendix A; see also Zolitschka 2003). Such high temporal resolution and accuracy were required in order to integrate instrumental and paleo data from multiple cores. Sampling and dating details of Lake Annecy were described in Perga et al. (2010).

Subfossil cladocerans analysis

Cladoceran remains (counts and measures) were analyzed as in Alric and Perga (2011). *Daphnia* (*D. longispina* species complex) were identified at the generic level (*Daphnia* sp.). Sididae, Cercopagidae, Leptodoridae, and *Bosmina* were identified at the species level and Chydoridae at the family level. Results were reported as number of subfossil remains per unit mass of dry sediment (remains/g dry mass) and per net accumulation rate (remains $\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) for each taxon. The length of *Daphnia* sp. post-abdominal claws was measured on a hundred remains for each sediment sample in order to estimate changes in the size structure of the *Daphnia* sp. population (Perga et al. 2010, Alric and Perga 2011). The length of *Daphnia* sp. post-abdominal claws was further used as a proxy of the modification in fish predation pressure on zooplankton for the three lakes (Perga et al. 2010), since predation by fish has a structuring effect on cladoceran body size (size-efficiency hypothesis [Brooks and Dodson 1965]).

Climatic data and proxy for changes in lake nutrient concentrations

For each lake, data sets of annual, winter, and summer air temperature as well as precipitations have been extracted from the gridded HISTALP data set (Auer et al. 2007), according to lakes geographical coordinates (data available online).⁵ The HISTALP database is based on a monthly homogenized long-term series of temperature, precipitation, and other meteorological variables for the Greater Alpine Region (4°–19° E, 43°–49° N, 0–3500 m above sea level). The air temperature and precipitation records extend both back

to before the year 1800 and thus completely covers the time period of the sediment record of our three lakes. Temporal changes in annual water [TP] of the three lakes were reconstructed using a diatom-transfer function (Appendix B).

Statistical analyses

Temporal trends in annual, winter, and summer air temperature as well as precipitation were tested using Mann Kendall's tau test. Chronological clustering analyses, computed from Bray-Curtis dissimilarity indexes, were performed on biostratigraphic sequences of sediment cores LEM10_P801 (Lake Geneva), LDB09_P301 (Lake Bourget), and 06-03 (Lake Annecy; see Perga et al. 2010) to reveal the timing of major changes in the cladoceran communities for all three lakes (CONISS in R package rioja [Juggins 2009]). The number of statistically significant biozones was assessed using the broken-stick approach (Bennett 1996). Significant changes in the abundance of each taxon between adjacent zones were thereafter tested, using nonparametric tests to avoid problems related to data heteroscedasticity and non-Gaussian distribution (Kruskal-Wallis tests accounting for Bonferroni's corrections; for conciseness, extensive results are not shown in the Results section).

Patterns of cladoceran community change were summarized using principal component analysis (PCA) of relative abundance data after Hellinger transformation (Legendre and Gallagher 2001). The first two principal components (PC) were identified as explaining significant proportions of the variance in the species data when compared with those expected under the broken-stick distribution. The scores on the first two PC were retained as dependent variables for subsequent modeling. A generalized additive model (GAM; Hastie and Tibshirani 1990) was then used to investigate the relationships between the trajectory of cladoceran community and external forcings as well as to separate and quantify their influences. GAM is a semi-parametric regression technique with the main advantage of not being tied to a particular functional relationship (i.e., linearity) and to be less restrictive in assumptions about the underlying statistical distribution of the data. In GAM, predictors (covariates) are assumed to affect the response variable through an additive sum of smooth functions. GAM parameterization and adaptation to paleoecological data were performed following Simpson and Anderson's (2009) technical recommendations. The feature selection process was based on a shrinkage method by a double penalty approach instead of the more commonly used stepwise procedure (Marra and Wood 2011). In our study, climate data (HISTALP data set), diatom-inferred TP, and *Daphnia* sp. claw size (as a proxy for changes in fish predation pressure) were introduced as the predictor variables in the model while the changes in the scores of the first two PCs were considered as the response variables.

⁵ www.zamg.ac.at/histalp/

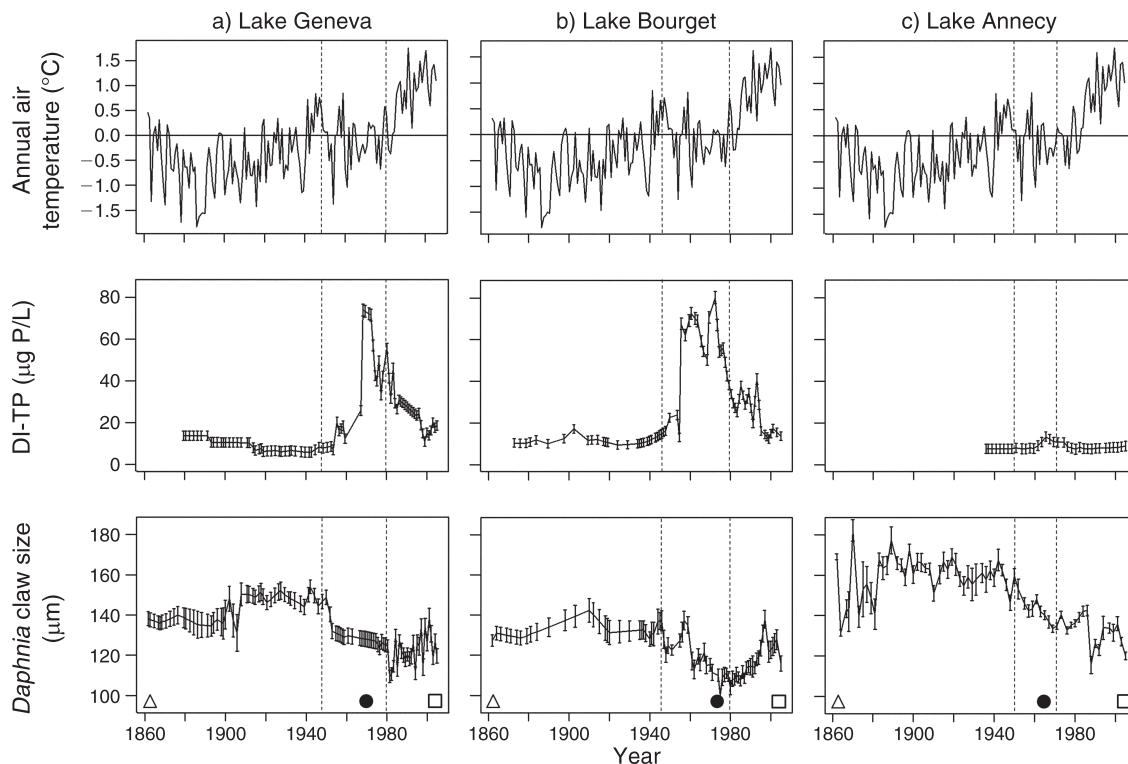


FIG. 1. Temporal changes in average annual air temperature (anomalies from the 1901–2000 average), diatom-inferred total phosphorus (DI-TP), and the length of *Daphnia* claws in (a) Lake Geneva, (b) Lake Bourget, and (c) Lake Annecy. Symbols correspond to the periods of pre-eutrophication (open triangles), eutrophication (solid circles), and re-oligotrophication (open squares). These time periods are characterized by changes in intensity of the different external forcings. Error bars represent \pm SE.

PCA and GAMs were performed on R2.11.0 statistical software (R Development Core Team 2009) using the vegan package (Oksanen et al. 2010) and mgcv package (Wood 2008, 2011) for R, respectively.

RESULTS

External forcings

In all three lakes, mean annual air temperature exhibited a common and significant increasing trend from the late 1980s. Between 1986 and 2009, the mean annual air temperature has increased by more than 1°C as compared with the prior period for all lakes (Fig. 1a–c). Increased annual air temperature essentially resulted from warmer winters (+1.6–1.7°C). Since no trend was observed for mean annual precipitation on the three lakes (Mann Kendall's tau test, $P > 0.05$), only mean air temperature was used in the following to account for climate change.

The reconstructed diatom-inferred TP (DI-TP) indicated that, for all three lakes, [TP] values were $< 10 \mu\text{g P/L}$ before the 1940s (pre-eutrophication period) when the first symptoms of eutrophication started (Fig. 1a–c). DI-TP increased first weakly from the 1940s (early eutrophication period), then dramatically from the 1960s (intense eutrophication period) in all three lakes. Maximum DI-TP were reached in the late 1960s for

Lake Annecy ($14 \mu\text{g P/L}$), the early 1970s for Lake Geneva ($70 \mu\text{g P/L}$), and the mid 1970s for Lake Bourget ($80 \mu\text{g P/L}$). The progressive decreases in DI-TP, resulting in values of [TP] $< 20 \mu\text{g P/L}$ in the late 2000s for Lakes Geneva and Bourget and $< 10 \mu\text{g P/L}$ for Lake Annecy, were in agreement with monitored dynamics of annual water [TP] (Appendix B).

In all three lakes, the average size of *Daphnia* sp. post-abdominal claws was large during the pre-eutrophication period and started to decrease from and all over the eutrophication period (Fig. 1a–c). *Daphnia* sp. post-abdominal claws got about 20% smaller as compared to the pre-eutrophication period in average, across all three lakes, hence suggesting that eutrophication triggered an increased fish predation pressure on zooplankton. Changes in *Daphnia* sp. size (and thus fish predation pressure on zooplankton) during the re-oligotrophication period yet diverged between lakes: *Daphnia* sp. size kept on shrinking in Lake Annecy, while *Daphnia* sp. size remained low but stable in Lake Geneva. In contrast, *Daphnia* sp. size increased back in Lake Bourget during the re-oligotrophication period, suggesting of a released fish predation pressure on *Daphnia* sp.

Trajectories of the cladoceran communities in lakes

Overall, the cladoceran remains retrieved from the sediment cores originated from six pelagic taxa (*Daphnia*

sp., *Bosmina longirostris* (O.F. Müller 1776), *Eubosmina coregoni* (Baird 1857), *Eubosmina longispina* (Leydig 1860), *Bythotrephes longimanus* (Leydig 1860) and *Leptodora kindti* (Focke 1844) as well as one littoral taxon (*Sida crystallina* (O.F. Müller 1776)) and two littoral subfamily (Aloninae and Chydorinae) of the Chydoridae family. Because the number of remains for Aloninae and Chydorinae was low, they were pooled in a single group (i.e., Chydoridae). All eight taxa were found in Lakes Geneva and Bourget but littoral and predatory cladocerans were not detected in Lake Annecy sediment records. Chronologically constrained cluster analyses identified five cladoceran assemblage zones for Lakes Geneva and Bourget and four zones for Lake Annecy (Fig. 2a–c), which matched the time periods of major [TP] changes in all three lakes. Cladoceran assemblages in zones 1, 2, and 3 (corresponding to pre-, slow, and intense eutrophication) showed changes in their structure that were similar between lakes. Thereafter, cladoceran trajectories diverged from the zone 4 corresponding to the beginning of gradual decrease in [TP].

In zone 1 (before the 1940s for all lakes, corresponding to the pre-eutrophication period), *Daphnia* sp., *E. longispina*, and *S. crystallina* remains were found in low abundance but exhibited the greatest contribution to total assemblages. *Bosmina longirostris* and *E. coregoni* were rare and found only in Lakes Geneva and Bourget.

Zones 2 (before the 1960s for Lakes Geneva and Bourget and the mid 1950s for Lake Annecy; slow eutrophication) and 3 (during the 1970s for Lakes Geneva and Bourget and the 1960s for Lake Annecy; intense eutrophication) were characterized by (1) a significant increase of *Daphnia* sp. abundance (from 6- to 12-fold) and (2) shifts in the composition of *Bosmina* remains toward *B. longirostris* dominance (Fig. 2a–c). *Bosmina* sp. (*E. longispina* in the three lakes plus *E. coregoni* in Lake Geneva and Bourget) abundances further increased during the eutrophication period. During this period also, *S. crystallina* abundance decreased steadily in the three lakes and Chydoridae abundances increased in Lakes Geneva and Bourget (Fig. 2a, b).

Zone 4 (from the 1980s for Lakes Geneva and Bourget and the 1970s for Lake Annecy) corresponded to time periods of decreasing [TP] for all lakes but also coincided with the beginning of significant changes in mean annual air temperature. At this stage, the responses of the cladoceran communities diverged between the three lakes. *Daphnia* sp. abundance started decreasing in all three lakes with different magnitudes (Fig. 2a–c). Lake Bourget exhibited the largest decrease (–74%), followed by Lake Geneva (–59%), and then Lake Annecy (–23%). The total abundance of *Bosmina* (*E. longispina* and *B. longirostris* in the three lakes plus *E. coregoni* in Lakes Geneva and Bourget) remained higher (from 2- to 10-fold), even in zone 5, than in the pre-eutrophication period, but the dynamics of the

different *Bosmina* species varied between lakes. *Eubosmina longispina* remained the dominant *Bosmina* species throughout this time period in Lakes Annecy (66% of the total *Bosmina* population) and Geneva (on average 89% of the total *Bosmina* population in zone 4 and 5) while *B. longirostris* made up a significant share of the *Bosmina* population in Lake Bourget. Moreover, the contributions of predatory cladocerans, *L. kindti* and *B. longimanus*, to total assemblages were much higher in Lakes Geneva and Bourget in zone 5 than at any other time zone. These species were not detected in Lake Annecy sediment core (Fig. 2a–c).

Additive models

Prior to the additive models, PCA was performed for each lake over the taxa abundance data sets. The first two axes of PCA accounted for 66%, 59%, and 93% of the total variance in cladoceran assemblages respectively in Lakes Geneva, Bourget, and Annecy and consistently separated samples according to zones determined by the previous cluster analyses (results not shown). The measure of the importance of each variable (i.e., the different cladoceran taxa) in accounting for the variability in the first and second principal components (PC1 and PC2) are presented in Table 1. Briefly, in Lakes Geneva and Bourget, one PC (PC2 and PC1, respectively) accounted for the correlated changes in the contributions of *Bosmina* sp. and predatory cladoceran species while the other PC (PC1 and PC2, respectively, for Lakes Geneva and Bourget) essentially accounted for the negatively correlated changes in *Daphnia* sp. contribution to total assemblages vs. that of littoral species. For Lake Annecy, PC1 represented changes in the composition of *E. longispina* and *S. crystallina* while PC2 accounted for the negatively correlated changes in *Daphnia* sp. contribution to total assemblage vs. that of *B. longirostris*. Analyses of biostratigraphic sequences, PCA and even GAMs were similar whatever the considered unit for cladoceran remains (abundance in remains/g dry mass) or fluxes (remains-cm⁻²·yr⁻¹).

The final models selected external forcings as covariates that differed among lakes for both PCs and explained between 35–87% of the deviance of PC1 and PC2 scores (Appendix C). The fitted relationships between PC1 or PC2 scores and the different predictors were either nonlinear (effective degrees of freedom [edf] > 1) or linear (edf = 1) according to the lake, PCs, and predictors (Appendix C).

In the three lakes, all three covariates contributed significantly to fitted PC1 and PC2 scores, although their respective importance changed between lakes and PCs (Fig. 3a–c; Appendix C). First, the contribution of annual air temperature to fitted PC scores was always higher in Lakes Geneva and Bourget than in Lake Annecy. Actually, fitted scores for Lake Annecy were essentially determined by covariates related to local forcings ([TP] and predation pressure) and the contribution of the climate component was rather low and

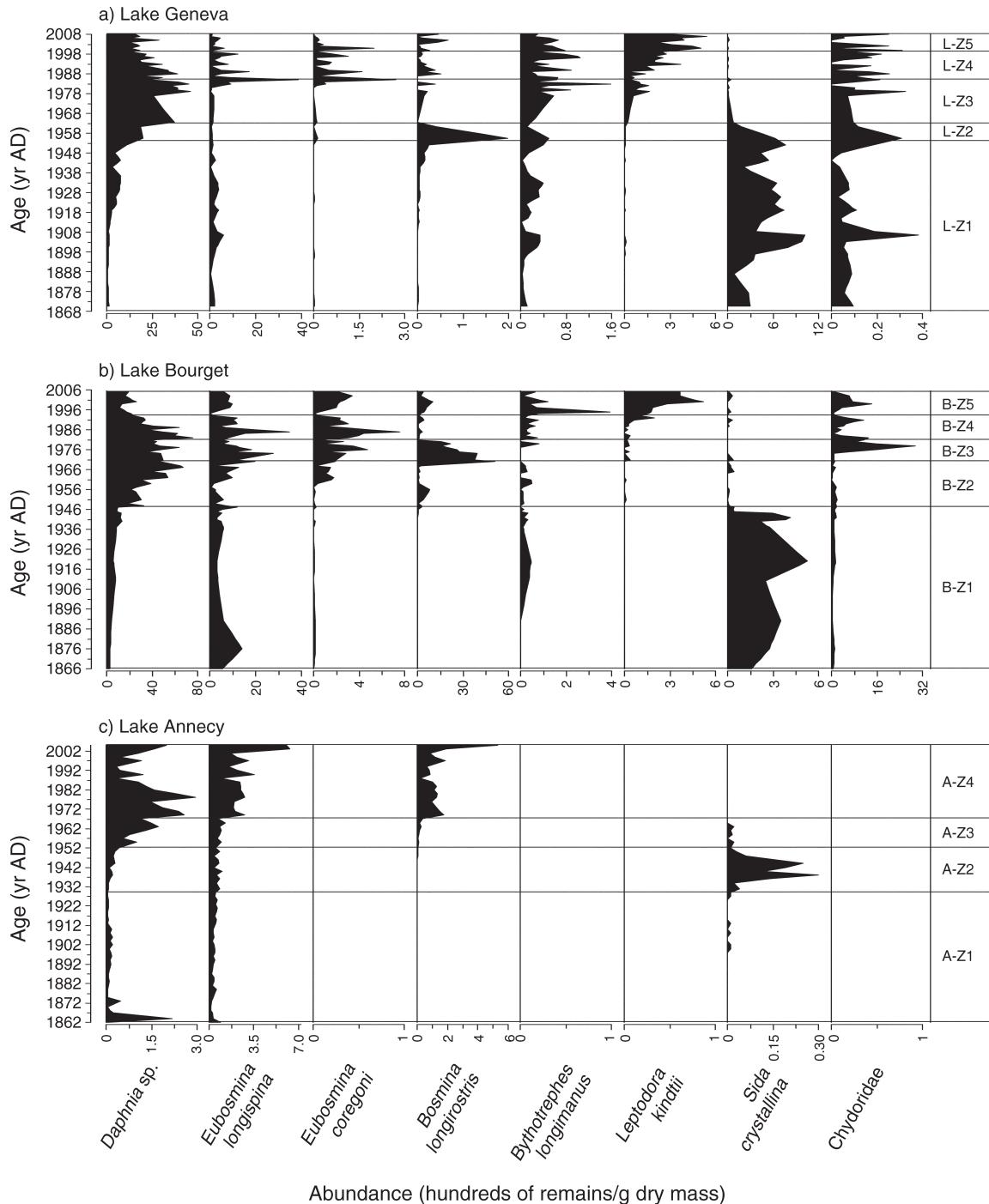


FIG. 2. Stratigraphic abundance of cladoceran remains in sediment cores (as absolute concentration per unit mass of dry sediment) of (a) Lake Geneva, (b) Lake Bourget, and (c) Lake Annecy. Zones (listed on left side of each panel) correspond to the time periods identified by chronological clustering on core LEM10_P8 for Lake Geneva, LDB09_P3 for Lake Bourget, and 06-03 for Lake Annecy.

only significant on PC2 (driving negative PC2 scores, i.e., promoting *B. longirostris* over *Daphnia* sp.). In both Lakes Geneva and Bourget, [TP] was one the major contributor to fitted PC scores, acting mostly by favoring *Daphnia* sp. vs. littoral species (PC1 and PC2

for Lakes Geneva and Bourget, respectively; Fig. 3a, b; Appendix C). The second series of fitted PC scores, corresponding to high abundances of *Bosmina* and predatory cladocerans (i.e., PC2 and PC1 for Lakes Geneva and Bourget, respectively), were essentially

driven by predation pressure and mean annual air temperature in Lake Geneva while similar cladoceran dynamics were driven by mean annual air temperature and [TP] in Lake Bourget (Fig. 3a, b; Appendix C).

The relative magnitudes according to which each covariate contributed to fitted PC scores differed between Lakes Geneva and Bourget but the temporal dynamics of their contribution were similar: [TP] contributed for almost all over the study periods while the influence of fish predation pressure was more temporally limited. In addition, in both lakes, significant influence of mean annual air temperature occurred from the late 1980s. Differences between the two lakes arose from the different covariate interactions. In Lake Bourget, the contribution of predation pressure was coupled, over the whole study period, to [TP], suggesting a correlation between these two forcings. In Lake Geneva, the contribution of predation pressure was coupled with that of [TP] from the late 1950s to the mid 1980s, i.e., periods of drastic changes in [TP], and from the late 1980s with that of mean annual air temperature. In Lake Annecy, the effect of predation pressure on changes of PC1 and PC2 scores was significant all over the study period with significant shift in the 1950s for PC1 scores as well as in the 1960s and the mid 1980s for PC2 scores. In addition, the contribution of predation pressure was coupled with that of [TP] from the 1960s to the late 1970s, while it was coupled with the contribution of mean annual air temperature from the mid 1980s.

DISCUSSION

Our study intended to evaluate and hierarchize the effects of local forcings vs. climate warming on the trajectory of cladoceran communities in three temperate, peri-alpine lakes submitted to similar climate change. Among the two local forcings considered herein, one acts essentially through bottom-up processes (nutrient concentrations) while the other one acts through top-down processes (fisheries management practices). Since effects of top-down controls are supposed to be strongest at the highest trophic levels and tend to fade out when going downward to lower trophic levels (and because the reciprocal is also true for bottom-up controls [McQueen et al. 1986, 1989]), we figured that primary consumers might provide a better picture of controls on the pelagic food web than primary producers. Hence, a paleoecological approach based on cladoceran sub-fossil remains was favored over the most commonly used diatom frustule remains.

A first limit to paleoecological approaches lies in the representativity of fossil assemblages as compared to their source communities. Potential differences in the cladoceran trajectories observed between lakes and/or changes along cores in the composition of the cladoceran remains could result from varying taphonomical bias or archiving processes between lakes and/or over time, rather than from actual ecological changes in the source communities. A previous sediment trap experi-

TABLE 1. Coefficient correlation (PC loadings) between the scores of the two principal components (PC1 and PC2) and the original variables (i.e., the different cladoceran taxa) for all three lakes.

Lake	Taxa	PC1	PC2
Lake Geneva	<i>Daphnia</i> sp.	0.479	
	<i>B. longirostris</i>		0.458
	<i>E. coregoni</i>		-0.462
	<i>E. longispina</i>		-0.496
	<i>B. longimanus</i>		-0.387
	<i>L. kindti</i>	0.405	
	<i>S. crystallina</i>	-0.489	
Lake Bourget	Chydoridae	-0.354	
	<i>Daphnia</i> sp.		0.610
	<i>B. longirostris</i>	-0.409	
	<i>E. coregoni</i>	-0.377	
	<i>E. longispina</i>	0.414	
	<i>B. longimanus</i>		-0.091
	<i>L. kindti</i>	-0.384	
Lake Annecy	<i>S. crystallina</i>	0.528	
	Chydoridae		-0.452
	<i>Daphnia</i> sp.		0.628
	<i>B. longirostris</i>		-0.544
	<i>E. longispina</i>	-0.533	
	<i>S. crystallina</i>	-0.542	

Note: PC loadings measure the importance of each variable in accounting for the variability in the PCs.

ment conducted in a nearby deep peri-alpine lake underpinned that the morphology of these deep, concave lakes favors a rather direct and faster sedimentation, and thus archiving, of cladoceran remains (Alric and Perga 2011). As a consequence, the cladoceran sediment records in these lakes exhibit high compositional fidelity. Yet, while all eight taxa were found in Lakes Geneva and Bourget, no remains for littoral and predatory cladocerans were detected in Lake Annecy sediment records, although some of them are present within the living community of this lake. The absence of such taxa in the sediment record may be due to lower abundances of total remains for time periods preceding the 1940s (whole sediment samples were counted but total number of remains were at some occasions <400, Perga et al. 2010). In addition, these taxa are generally less represented in Lake Annecy as compared to the two other lakes (for instance, predatory cladocerans made up <0.9% of the whole cladoceran abundance in Lake Annecy in 2011, but 2–4% in Lakes Geneva and Bourget; M.-E. Perga, unpublished data). Rare cladoceran species (<1%) are typically no or poorly represented in fossil assemblages (Frey 1986, Kattel et al. 2007, Nykänen et al. 2009). So, overall differences in the cladoceran remains composition between lakes essentially mirror actual differences in the relative abundance of species in their living communities. Besides, further degradation of some of the most sensitive remains, once buried in sediment, might create a tendency to higher abundances toward the uppermost part of cores, artifactually interpreted as increased abundance of these

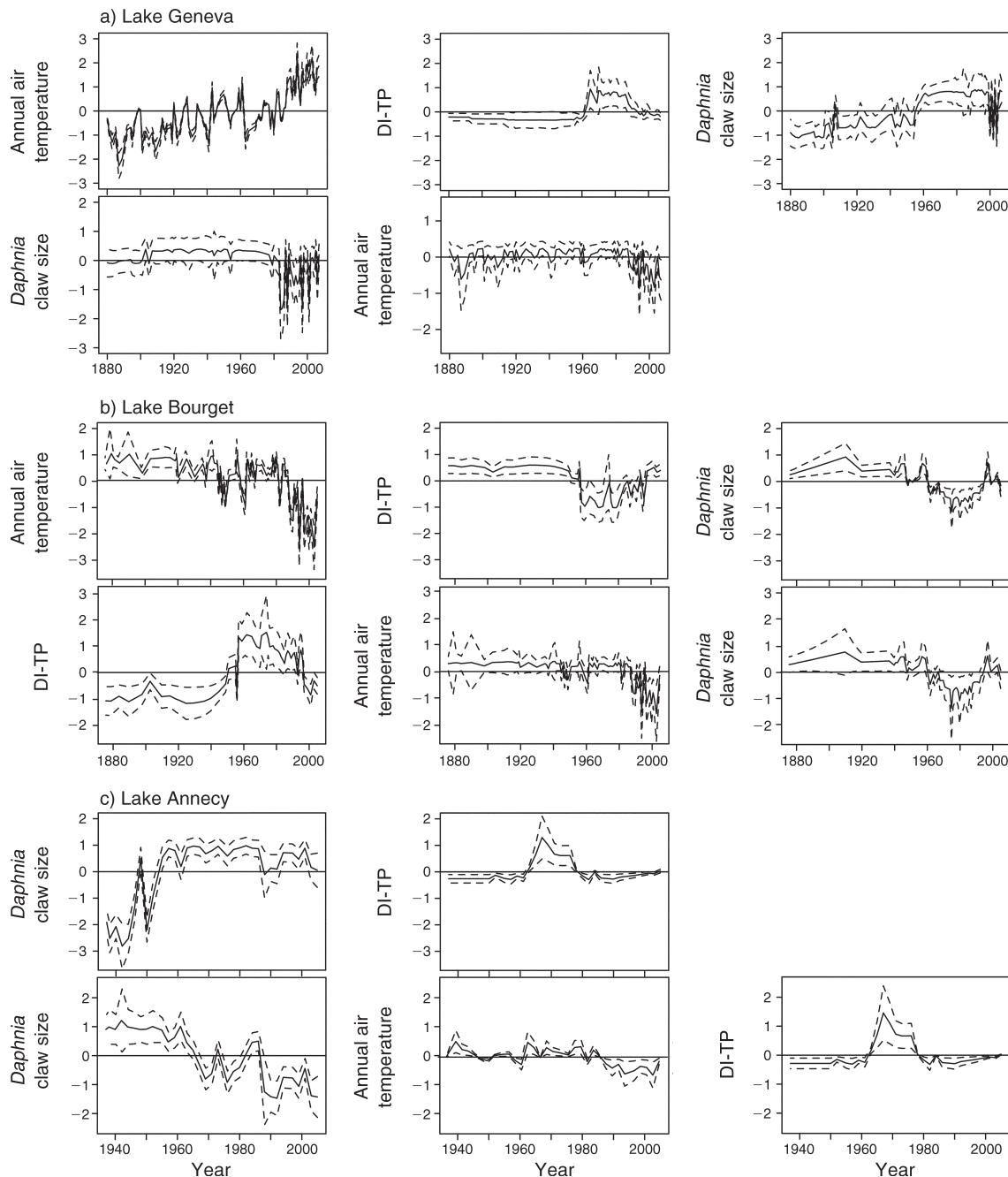


FIG. 3. Temporal contribution of covariates selected in final GAMs fitted to cladoceran principal components scores PC1 (upper panels) and PC2 (lower panels) for (a) Lake Geneva, (b) Lake Bourget, and (c) Lake Annecy. The dashed lines indicate the approximate 95% point-wise confidence interval on the contribution. Where the dashed lines include the zero lines, the contribution of the covariate is not statistically significantly different from the intercept. The order of covariates for each lake corresponds to the importance of the contribution to explain the fitted cladoceran PC scores (see Appendix C for more details).

taxa over the most recent times. This should be evoked for *L. kindti*, the remains of which (mandible and caudal furca) are known for being fragile and easily broken. Yet, the comparison of trends observed in the sediment record with those monitored since 1974 in Lake Geneva, confirmed that the abundance of this particular taxa in

the water column has increased two- to three-fold over the last 40 years (Molinero et al. 2007), as very accurately mirrored in the sediment record. Hence, the sediment archives provided a faithful picture of the changes in the cladoceran community structure over time and between lakes.

Except for climate, for which direct data was available, our approach also required paleolimnological reconstructions for the forcings considered herein. Within paleolimnological approaches, past [TP] has been quite usually inferred from diatom remains (Hall and Smol 1992). Because some long-term monitoring data were also available, we were able to compare DI-TP to measured water [TP]. Both were globally consistent and highly correlated (Appendix B). On some occasions, DI-TP were over-estimated but the availability of monitored [TP] as well as the comparison with several other paleo-proxies allowed correcting for these inconsistencies. Overall, the confidence in TP reconstructions is relatively good. The challenge was essentially in the reconstruction of the third forcing factor included within this study, i.e., a proxy related to fisheries management practices. Unfortunately, neither long-term data for fish stocking, nor catch per unit effort (CPUE) were available over the study periods. Temporal changes in fisheries practices and regulations were then approached through changes in fish predation pressure on zooplankton, and more specifically on *Daphnia* sp. This proxy relied indirectly on the size-efficiency hypothesis (Brooks and Dodson 1965), i.e., that fish predation pressure exerts a strong structuring impact on the body size of their preys (Kerfoot 1981, Gliwicz and Wrzosek 2008). Indeed, such a relationship between fish stocks and prey size structure has already been used to infer past abundances of zooplanktivorous fish from the size of *Daphnia* sp. ephippia in a set of 52 shallow lakes from Denmark, Greenland, and New Zealand (Jeppesen et al. 2002). Such a relationship also holds for our three study lakes since we could show that the temporal changes in *Daphnia* sp. body size were strongly inversely correlated with fisheries catches in the main zooplanktivorous species (Spearman's rank correlation test between *Daphnia* sp. claws size and catches; Lake Geneva, $\rho = -0.511$, $P = 1.58 \times 10^{-6}$; Lake Bourget, $\rho = -0.340$, $P = 0.009$; Lake Annecy, $\rho = -0.426$, $P = 0.008$; Appendix D), confirming that even though other environmental conditions such as food quality/quantity or temperature (Hart and Bychek 2011) and invertebrate predation (Branstrator 2005), can affect *Daphnia* sp. body size, they may not be strong enough to compromise the relevancy of using *Daphnia* sp. body size as a proxy for fish predation pressure. In addition, as evidenced by *Daphnia* sp. responses in re-oligotrophication periods in all three lakes, changes in *Daphnia* sp. body size were independent from those in their (absolute or relative) abundances, excluding any circularity in using *Daphnia* sp. body size to predict the whole cladoceran composition over time.

Hence, despite such limits, results presented here reveal that long-term changes in cladoceran communities of Lakes Geneva, Bourget, and Annecy, have been driven by a set of complex interactions between climate, nutrient status, and intensity of fish planktivory.

External forcings regulating cladoceran communities over the long term

The paleolimnological reconstructions showed that cladoceran communities of the three lakes exhibited similar trajectories until the 1980s, but then diverged. GAMs for their part showed that, depending on time periods, trajectories of cladocerans were driven by different combinations of forcings.

Before the 1980s, P was the main driver of the pelagic food web. Increasing [TP] from the 1940s triggered similar changes in the cladoceran community structure although maximum [TP] levels differed between lakes. Through a bottom-up effect, increasing [TP] allowed the increase of pelagic cladoceran abundance (McCauley and Kalff 1981), in particular *Daphnia* sp., and resulted in a drastic decline in species more typical for shallow habitats (*S. crystallina*) due to lower water transparency and reduction of littoral habitats. Consistent patterns were observed in other deep peri-alpine lakes (Ravera and Parise 1978, Manca et al. 2007). In all lakes, decreasing *Daphnia* sp. body size coincided with the onset of eutrophication, attesting that the intensity of top-down control by planktivorous fish increased with higher nutrient concentrations. Another striking pattern at this same time period was the appearance of *B. longirostris* and sometimes dominance within the *Bosmina* population. Such transition was actually postulated to result from an indirect predation-mediated effect (i.e., reducing of the competitive interaction between *Bosmina* sp. and *Daphnia* sp. under a high fish predation pressure) rather than from a direct effect of increased nutrient inputs on the genus *Bosmina* (Brooks 1969, Kerfoot 1974). Our results support this hypothesis, because the appearance of *B. longirostris* coincided with the beginning of *Daphnia* sp. size reduction in the late 1940s. This interpretation is consistent with indirect facilitation processes previously tested in mesocosms (Vanni 1987). Despite fish being regularly stocked in all three lakes beginning in the 1920s, evidence for strong fish predation pressure only appeared in the 1940s when lake nutrient concentration increased and could sustain an increased fish population. Therefore, although fish predation pressure exerted a strong structuring effect on the cladoceran community structure before 1980, this top-down control was, in fine, possible because of increased lake productivity.

In contrast, beginning in the 1980s, GAM results highlighted that decreasing nutrient concentrations were not the only forcing explaining changes in cladoceran communities in all three lakes. Actually, only *Daphnia* sp. abundance was driven by [TP] and hence responded to reduced nutrient inputs. In contrast, the dynamics of all the other cladoceran taxa seemed to be determined by other forcings. Indeed, *Bosmina* sp. abundance remained relatively high although nutrient concentration dropped. In addition, the abundance of *L. kindti* and *B. longimanus* increased in Lakes Geneva and Bourget. Consequently, decreasing [TP] in all three lakes did

not result in reverse trajectories for the cladoceran communities. Such a lack of recovery to the pre-eutrophication community structure has been observed in other European lakes for which the re-oligotrophication period coincided with a period of air warming as a result from positive phase of North Atlantic Oscillation. In such lakes, these trajectories have been attributed to climate change (e.g., Jeppesen et al. 2007, Søndergaard et al. 2007). Yet, while all three studied lakes have also been undergoing similar warmer air temperature during the last 25 years, results emphasized that they were not equally sensitive to climate change, but also that their subsequent responses to warming differed.

To what extent can climate explain the lack of recovery to pre-eutrophication state?

GAM results underpinned a significant implication of warming to changes in cladoceran communities in the three lakes, but the climate contribution to the cladoceran dynamics was contrasted between lakes. In Lake Annecy, major changes in the cladoceran community structure after the 1980s occurred as changes in the relative proportions of *Bosmina* sp. and *Daphnia* sp., and these changes could not be related only to any obvious climate warming effect. These conclusions are strengthened by a recent study that showed, from monitoring data, that the cladoceran succession pattern in Lake Annecy was less sensitive to the 2003 heat wave in contrast to Lake Geneva where it was deeply affected (Anneville et al. 2010). The continuous shrinking of the *Daphnia* sp. population over the last 60 years and the persistence of an abundant *Bosmina* sp. population in Lake Annecy actually result from a still-increasing fish predation pressure on zooplankton, artificially maintained through annual whitefish stocking until 1997. In this lake, changes in fish planktivory as a result of fisheries management practices might outweigh the impact of global warming. So, in Lake Annecy, climate acted marginally on the cladoceran community, while it has been exerting a major structuring effect over the last 30 years in Lakes Geneva and Bourget. However, since part of the response to climate in Lakes Geneva and Bourget occurred through predatory cladocerans, the lowest contribution of climate to the cladoceran trajectories observed in Lake Annecy might partly arise from the lack of recording of predatory cladocerans in its sediment archives. To test how much differences in lake vulnerability to climate were dependent on predatory cladocerans, another series of GAMs, including only *Daphnia* sp. and *Bosmina* sp. in the response variable, were conducted (Appendix E). The ranked contributions of the forcings to the observed trajectories were very similar in these additional GAMs to those performed on the whole data sets, showing that the differences in lake vulnerability to climate warming is not artifactual and poorly depends on predatory cladocerans. This comparison also underpinned that predatory cladocerans make up only a minor part of the

cladoceran responses to warming, which essentially occurs through an increased contribution of some *Bosmina* species (*B. longirostris* and *E. coregoni*, for Lakes Geneva and Bourget) and a higher *Bosmina* sp. to *Daphnia* sp. ratio (Lakes Geneva and Annecy).

Not only the contribution, but also the pathways according to which climate has been impacting cladoceran communities, differed between the three lakes. Air temperature was, from the 1980s, a significant contributor to PC scores in all the three lakes. The direction of correlations suggested a positive effect of warmer temperatures on the abundance of *Bosmina* species, *L. kindti*, and more moderately on *B. longimanus* in Lakes Geneva and Bourget, and, to a lesser extent and only on *B. longirostris*, in Lake Annecy. These results support the hypothesis of a direct effect of climate on cladoceran communities through physiological processes. Indeed, *Bosmina* sp. generally presented a faster development and growth than *Daphnia* sp. and warming is expected to emphasize this difference (Vijverberg 1980). In addition, longer stratification periods should promote the thermophilic taxa such as *L. kindti* and *B. longimanus* (Wagner and Benndorf 2007, Manca and DeMott 2009). In Lake Bourget, GAM did not highlight any clear interaction between climate and local forcings. Hence, the latter might be the major pathway under which climate has been influencing the cladoceran community structure. More indirect ones cannot be excluded though. Indeed, the effect of increased air temperature could also involve trophic processes and competition between *Bosmina* sp. and *Daphnia* sp., through alterations of the composition of primary producers. For instance, climate warming is suspected of promoting a summer bloom of filamentous algae (Paerl and Huisman 2008) and blooms of the filamentous cyanobacteria *Planktothrix rubescens* have been observed in Lake Bourget from the 1990s (Jacquet et al. 2005). The filamentous morphology of cyanobacteria is thought to be more detrimental to food-collection mechanisms of larger filter-feeding species (Haney 1987), hence conferring a trophic competitive advantage to *Bosmina* sp. over *Daphnia* sp. (Gliwicz 1990).

In Lake Geneva, but also marginally in Lake Annecy, the contribution of increased air temperature to PC scores was shown to be coupled and positively related to fish predation pressure from the late 1980s. Climate warming might, thus, also exert a more indirect structuring effect on cladoceran communities, by increasing the top-down control in these lakes. This was highlighted by the persistence of small *Daphnia* sp. during re-oligotrophication in these two lakes, with subsequent implications for competition with *Bosmina* sp. Hence, in Lakes Geneva and Annecy, and in contrast to Lake Bourget or to the eutrophication period, the intensity of fish predation pressure was decoupled from lake nutrient status from the late 1980s. Indeed, warming was shown to benefit to whitefish recruitment (Eckmann and Rösch 1998) and thus to stocking

(Gerdeaux et al. 2006). However, the interaction between fish predation pressure and climate warming occurred only in two of the lakes, although all three are stocked with whitefish. These were the lakes in which whitefish is stocked every year as yolk-sac larvae. No such interaction was detected for Lake Bourget in which stocking occurs much later in the season, at juvenile stages (Champigneulle et al. 2001). These differences suggest that the stocking practices may also modulate cladoceran sensitivity and response to climate. Indeed, whitefish larvae stocked early in the season would exhibit a higher growth rate and lower predation losses due to warmer summers (Straile et al. 2007) and exert an even stronger predation pressure on the cladoceran compartment at the season at which it is very sensitive to top-down regulation (Cryer et al. 1986, Mehner and Thiel 1999) as compared to fish stocked at juvenile stages.

Local forcings affect lake sensitivity to climate change

In a number of ecosystems, climate change has been shown to interact with and to inflate deleterious consequences of local human stressors, resulting in a faster erosion of biodiversity (Benning et al. 2002), in a limited efficiency of restoration measures (Anneville et al. 2005, Jeppesen et al. 2007), in a distortion of the strength of trophic interactions (Hoekman 2010, Kratina et al. 2012), or in decreased ecosystem resilience (Buma and Wessman 2011). This issue, though, has rarely been considered the other way round, i.e., ecosystem sensitivity to climate might vary depending on existing local pressures (but see Palmer et al. [2008] for an example on river basins). In this study, we showed that three lakes subjected to similar climatic variability but different intensities of analogous local stressors show uneven susceptibility to climate warming. Cardille et al. (2009) archived similar conclusions when investigating carbon and water cycling in 7000 lakes under similar climate influence. In their study, varying lake sensitivity to climate was attributed to geomorphological or hydrological differences between systems, i.e., lake and watershed size, age, and upstream and downstream connections. Indeed, geomorphological characteristics are thought to modulate lake susceptibility to meteorological forcings, shallow lakes being more sensitive than deeper ones (George 2010). In our study, lakes were chosen in order to minimize geomorphological differences but it has to be acknowledged that their depth and size remain different (especially between Lake Geneva and the other two). Still, such size differences are not likely the main factor responsible for their uneven vulnerability to climate warming. Indeed, Lake Annecy is the smallest and the least deep of the study lakes. Since it is also rather sheltered from winds and poorly influenced by floods, Lake Annecy warms up quicker than the other two (Anneville et al. 2010). However, the cladoceran community structure, and by extension the pelagic food web, of Lake Annecy was

shown to be poorly responding to climate warming. A hypothesis might be that when nutrients (particularly P) are in a limiting range for the organisms' growth (i.e., oligotrophic status), competition for the resource rather than climate forcing will drive the community-level shifts. In Upper Lake Constance, another deep, temperate, peri-alpine lake with a current oligotrophic status, climate warming was considered as a major forcing of the phytoplankton productivity changes since the mid 1980s. However, simulations predicted that the ongoing decline in [TP] and further decreasing should outweigh climate effects on phytoplankton development in the foreseeable future (Stich and Brinker 2010). Consistently, such lack of sensitivity of the cladoceran community in Lake Annecy so far might be the consequence of its low nutrient concentration. In addition, the analysis of long-term data-series for phytoplankton of five deep temperate peri-alpine lakes revealed that mesotrophic, as compared to oligotrophic, lakes are those for which phytoplankton response (in terms of abundance) to climate is the strongest (Anneville et al. 2005) and this pattern might have consequences further up in the food chain. Indeed, the trajectories of cladoceran communities of the larger but more eutrophic Lakes Geneva and Bourget were substantially driven by climate warming. Lake nutrient status, inherited from its trophic history, is a local human stressor that is likely to strongly modulate lake vulnerability to climate warming.

The contribution of climate warming to cladoceran trajectories was, yet, also different among lakes of similar nutrient status, with a more marked influence on Lake Bourget than on Lake Geneva but also varying pathways. GAM results suggested a rather direct influence of climate warming on cladoceran community structure that was interpreted as a physiological response to warmer waters in both lakes. The contribution of this direct pathway was much stronger in Lake Bourget than in Lake Geneva but we believe these differences depend on geomorphological characteristics rather than from local pressures. Indeed, Lake Bourget warms up quicker than Lake Geneva every spring and reach higher surface temperatures (Jacquet et al. 2005), partly because of its smaller depth and lower hydrological influence of tributaries. Results, however, suggested that the impact of climate warming on cladoceran communities in Lake Geneva and Annecy could also occur along an indirect pathway, involving increased recruitment of zooplanktivorous fish following fisheries management practices. More intensive stocking but also release of different development stages in Lakes Geneva and Annecy, as compared to Lake Bourget, might explain the observed coupling between fish predation pressure and climate warming, hence highlighting that fisheries management is another local stressor that might modify pathways under which climate warming might impact ecosystems. To conclude, since local perturbations affect lake vulnerability and responses to climate

warming, they should be accounted for when trying to predict future impacts of climate change.

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SUPPLEMENTAL MATERIAL

Appendix A

Age models of reference cores and samples dating ([Ecological Archives E094-256-A1](#)).

Appendix B

Diatom-inferred total phosphorus (TP) annual concentrations ([Ecological Archives E094-256-A2](#)).

Appendix C

Contribution of various covariates to the generalized additive models (GAMs) fitted to cladoceran principal components PC1 and PC2 scores for each lake ([Ecological Archives E094-256-A3](#)).

Appendix D

Relationships between the *Daphnia* sp. body size and fish stocks ([Ecological Archives E094-256-A4](#)).

Appendix E

Additional GAMs including only *Daphnia* and *Bosmina* taxa in the response variable for the three lakes ([Ecological Archives E094-256-A5](#)).