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La vulnérabilité des lacs face au couplage du climat et des perturbations anthropiques locales : approche paléolimnologique basée sur les cladocères

Benjamin Alric

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THÈSE

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codirigée par **Marie-Elodie PERGA**

préparée au sein du **Laboratoire INRA-UMR 0042 CARTEL**
dans l'**École Doctorale Sciences et Ingénierie des systèmes,**
de l'environnement et des organisations

L'influence des perturbations locales sur la vulnérabilité et la réponse des réseaux trophiques pélagiques lacustres face au changement climatique : une approche paléo-écologique basée sur les cladocères

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“Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought seem to be the most effective of all checks. I estimated (chiefly from the greatly reduced numbers of nests in the spring) that the winter of 1854-5 destroyed four-fifths of the birds in my own grounds.”

CHARLES DARWIN – The Origin of Species

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Résumé

Les écosystèmes lacustres sont de plus en plus soumis à de multiples perturbations mais leur réponse est encore trop rarement considérée de façon globale. En effet, au travers d'un jeu d'interactions complexes, chaque perturbation peut moduler l'intensité de l'impact des autres sur les lacs, et de ce fait, leur réponse. Dans ce contexte, ce travail doctoral est axé sur l'approfondissement de notre compréhension de la réponse des lacs à un contexte de perturbations multiples, sur le long terme. Pour cela, trois grands lacs profonds (le lac Léman, du Bourget et d'Annecy), soumis à une perturbation régionale similaire (i.e., le réchauffement climatique) et à deux perturbations locales (i.e., les changements dans le statut trophique et dans les pratiques de gestion piscicole) d'intensités différentes, ont été choisis. La réponse de ces lacs à ces changements a été abordée au travers d'une approche paléolimnologique, basée sur les cladocères. En effet, la capacité de ceux-ci à intégrer les changements temporels dans le réseau trophique pélagique en réponse aux trois perturbations environnementales en fait un modèle adéquat pour reconstruire les changements à l'échelle de la communauté pélagique. Plus précisément, nous avons abordé (i) les changements dans les communautés de cladocères, au cours du siècle dernier, en réponse aux trois perturbations environnementales et (ii) l'impact de ces perturbations sur les stratégies de reproduction des Daphnies. Cependant, le manque de connaissance dans les grands lacs profonds sur la représentativité des communautés sources de cladocères par les assemblages de restes archivés dans les sédiments a tout d'abord conduit à faire un point méthodologique. Ce dernier a abouti à la mise en évidence de différences dans le niveau de représentation de communautés sources de cladocères selon le type de restes utilisés. La composition taxonomique et la structure en taille des restes parthénogénétiques (i.e., exosquelettes) reflètent relativement bien celle des communautés sources. Quant aux éphippies (œufs de dormance), elles se révèlent des indicateurs fiables pour reconstruire les comportements de reproduction. Suite à ces résultats, les reconstructions paléolimnologiques des communautés de cladocères montrent que leur trajectoire écologique était contrôlée par des interactions complexes entre les trois perturbations différentes, selon les périodes de temps et entre les lacs. De plus, la réponse des communautés de cladocères au climat était différente entre les trois lacs comme une fonction de l'intensité des forçages locaux. Ces observations suggèrent qu'il est important d'inclure le rôle des perturbations locales dans la prédiction de l'impact futur des changements climatiques sur les lacs. L'impact des perturbations environnementales sur le comportement de reproduction des Daphnies est tel que des événements d'hybridation interspécifique ont été observés. Cependant, ces événements d'hybridation sont issus de sensibilité aux trois perturbations environnementales différentes entre les espèces de Daphnies.

Mots clefs : Changement climatique, statut trophique, pression de prédation, relations trophiques, stratégie de reproduction, paléolimnologie, cladocères, lacs péri-alpins.

Abstract

Lake ecosystems are increasingly subjected to multiple perturbations but their response is too rarely considered in overall. But, through a complex set of interactions, each perturbation can modulate the intensity of the impact of each other on the lakes, and thus their response. In this context, this work is focused on deepening our understanding of the response of lakes in a context of multiple perturbations over the long time period. We studied this response performing a paleolimnological approach (based on cladoceran) on three large, deep lakes (Lakes Geneva, Bourget and Annecy) subjected to a similar regional perturbation (i.e., climate warming) and varying intensities of two local perturbations (i.e., changes in nutrient inputs and fisheries management practices). The ability of cladoceran to integrate the temporal changes in the pelagic food web in response to three environmental perturbations makes them a suitable model to reconstruct the changes in the whole pelagic community. Specifically, we addressed (i) changes in cladoceran communities, during the last century, in response to three environmental perturbations and (ii) the impact of these perturbations on reproductive behavior of *Daphnia*. However, the lack of knowledge in large, deep lakes on the representativity of source cladoceran communities by fossil assemblages in sediments firstly led to a methodological calibration. The latter showed that the representation level of source communities was different according to the type of remain. Parthenogenetic remain assemblages (i.e., exoskeleton) reflect accurately the taxonomical and size structure of source communities in contrast to ephippia which are reliable proxy to reconstruct reproductive behavior. Following these results, the paleolimnological reconstructions of cladoceran communities showed that their ecological trajectories are controlled by complex interactions between the three perturbations, according to time periods and lakes. Moreover, the response of cladoceran communities to climate warming was different between the three lakes as a function of the intensity of local forcings. These observations suggest that it is important to include the role of local perturbations in predicting the future impact of climate change on lakes. The impact of environmental perturbations on the reproductive behavior of *Daphnia* is such that interspecific hybridization events occurred. However, these hybridization events were the result of different sensitivity to perturbations among *Daphnia* species.

Keywords: Climate change, trophic status, predation pressure, trophic interactions, reproductive strategy, paleolimnology, cladoceran, subalpine lakes.

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I. Introduction

I.1. Contexte et problématique

Si les populations humaines, comme tout organisme, modifient leur environnement (Crutzen 2002), leur influence est telle que la majorité des changements environnementaux globaux actuels leur est imputée (Vitousek 1994, Vitousek et al. 1997, Tilman et Lehman 2001) et notamment les modifications climatiques enregistrées ces dernières décennies (Jones et al. 2001, Karl et Trenberth 2003, Rosenzweig et al. 2007). Ces changements climatiques ont des répercussions profondes sur les écosystèmes naturels, terrestres et aquatiques (e.g., Stenseth et al. 2002, Walther et al. 2002, O'Reilly et al. 2003, Parmesan et Yohe 2003). Les effets écologiques les plus marquants sont sans doute, à court terme, les changements structurels, avec principalement une perte de diversité biologique, qui peuvent affecter, en conséquence, le fonctionnement des écosystèmes et leur capacité à fournir des services écosystémiques (Vitousek et al. 1997). Si de nombreuses études observent et confirment l'impact du changement climatique sur la structure et le fonctionnement des écosystèmes naturels, relativement peu démontrent les voies et processus qui génèrent ces impacts. Par conséquent, notre compréhension des mécanismes par lesquels le climat affecte ces systèmes reste encore limitée (Keller 2007). Ces lacunes sont un véritable défi pour les scientifiques, d'autant plus que les impacts écologiques des forçages environnementaux, tel que le climat, devraient s'accroître dans un futur proche et que nous sommes confrontés de plus en plus à des contextes de perturbations multiples (Sala 2000, IPCC 2001, MEA 2005).

I.1.1. Les lacs : un modèle d'étude de l'impact du changement climatique sur les écosystèmes

La mise en évidence de l'impact des perturbations anthropiques sur les écosystèmes naturels nécessite des longues séries de données de suivis (supérieures à 50 ans, selon Elliott 1990, Magnuson 1990, Anderson 1995).

L'une des principales raisons est que ces longues séries temporelles donnent accès à l'état des écosystèmes avant même ces perturbations. Ces informations renseignent sur la "ligne de base". Elles permettent aussi d'évaluer les trajectoires de réponses des systèmes face à ces perturbations, et donc d'en comprendre les mécanismes, ce qui est crucial dans l'optique d'améliorer la prédiction de l'impact des changements environnementaux et par conséquent, l'élaboration de programmes de restauration durable (Bennion et Battarbee 2007, Jackson et Hobbs 2009, Bennion et al. 2011). En ce qui concerne les écosystèmes terrestres, les longues séries de données instrumentales se caractérisent principalement par des suivis sur des échelles de temps plus ou moins longues selon les sites (i.e., allant de quelques années à plusieurs dizaines d'années) et peuvent couvrir des aires géographiques relativement grandes (e.g., l'Europe occidentale et centrale) (Engler et al. 2011). De longues séries de données sont également disponibles pour certains lacs, mais trop rares sont ceux pour lesquels le suivi englobe les périodes d'intérêt (i.e., la période avant, pendant et après une perturbation) (Anderson 1995, Battarbee et al. 2005). De plus, quand elles sont disponibles, les données les plus anciennes peuvent être difficilement comparables avec le suivi actuel, du fait notamment de changements dans les méthodes de mesures.

Les sédiments lacustres présentent la caractéristique d'intégrer l'effet des changements climatiques sur les lacs ainsi que sur leur bassin versant et dans l'atmosphère (Williamson et al. 2009). En l'absence de perturbations structurales, l'accumulation des sédiments se déroule de telle manière que les couches de sédiments se superposent les unes sur les autres dans un ordre chronologique, de sorte qu'à un moment donné, une couche est plus récente que celle sur laquelle elle repose et plus vieille que celle qu'elle supporte. Ces couches sédimentaires renferment du matériel d'origine endogène dérivé du lac (e.g., des restes fossiles de cladocères, de diatomées, de chironomes,...) et d'origine exogène transporté dans le lac (e.g., des restes fossiles d'insectes, de pollen, du matériel minéral,...) (Smol et al. 2001a,b, Cohen 2003b). Les caractéristiques structurales et physicochimiques des sédiments lacustres en font des archives naturelles des états passés. L'approche paléolimnologique est donc une alternative pour reconstruire et comprendre les changements historiques des lacs (voir Smol 2008 pour des exemples).

Dans ces conditions, l'utilisation d'une approche paléolimnologique pour l'étude de l'impact écologique du climat sur les lacs a connu un certain intérêt de la part des scientifiques (e.g., Fritz 1996, Battarbee 2000, Smol et Cumming 2000, Koinig et al. 2002). Généralement, dans ces études, la réponse des lacs aux changements climatiques sur le long terme a été abordée selon deux approches fondées sur une idée commune, c'est-à-dire d'obtenir un signal de l'impact climatique en minimisant toute interférence potentielle liée, notamment, à l'influence des perturbations humaines locales. La première approche consiste à reconstruire les changements écologiques des lacs sur des échelles de temps millénaires, c'est-à-dire sur des périodes de temps englobant jusqu'à l'ensemble de l'Holocène (environ 15 000 ans) et caractérisées principalement par une variabilité climatique naturelle et un faible impact humain (e.g., Schmidt et al. 2002, Rasmussen et Bradshaw 2005, Schmidt et al. 2006, Catalan et al. 2009, Milecka et al. 2011). La deuxième approche (à l'échelle des deux derniers siècles) se concentre sur les lacs des régions polaires et alpines, isolés de toutes perturbations anthropiques locales/directes (e.g., Douglas et al. 1994, Battarbee 2000, Jones et Birks 2004, Battarbee 2005, Karst-Riddoch et al. 2005, Solovieva et al. 2008). De plus, ces lacs sont situés dans des régions où les conséquences du changement climatique sont très marquées (ACIA 2004, Meehl et al. 2007, Stroeve et Serreze 2008), avec un réchauffement trois à quatre fois supérieur à celui observé en moyenne à l'échelle du globe (de +1.5 à 2°C depuis 1980, comparés au +0.5°C à l'échelle du globe, Beniston et al. 1997).

1.1.2. Des impacts variés du changement climatique sur les lacs

Les résultats de ces nombreuses études peuvent à présent faire l'objet de synthèses dont l'objectif serait de souligner les grandes tendances de l'impact du climat sur ces systèmes isolés. Notamment, une méta-analyse des enregistrements sédimentaires de 55 lacs arctiques a montré sur les 150 dernières années que la réduction de la période de couverture de glace, liée à l'augmentation de la température, engendre de profondes modifications dans la composition taxonomique de la communauté de diatomées, avec un déplacement des stratégies de vie des habitats benthiques vers les habitats pélagiques (Smol et al. 2005). Le réchauffement climatique (sur le siècle dernier) affecte le régime thermique des lacs polaires et alpins, non seulement, par son influence sur la période de gel des lacs mais aussi lors de la stratification.

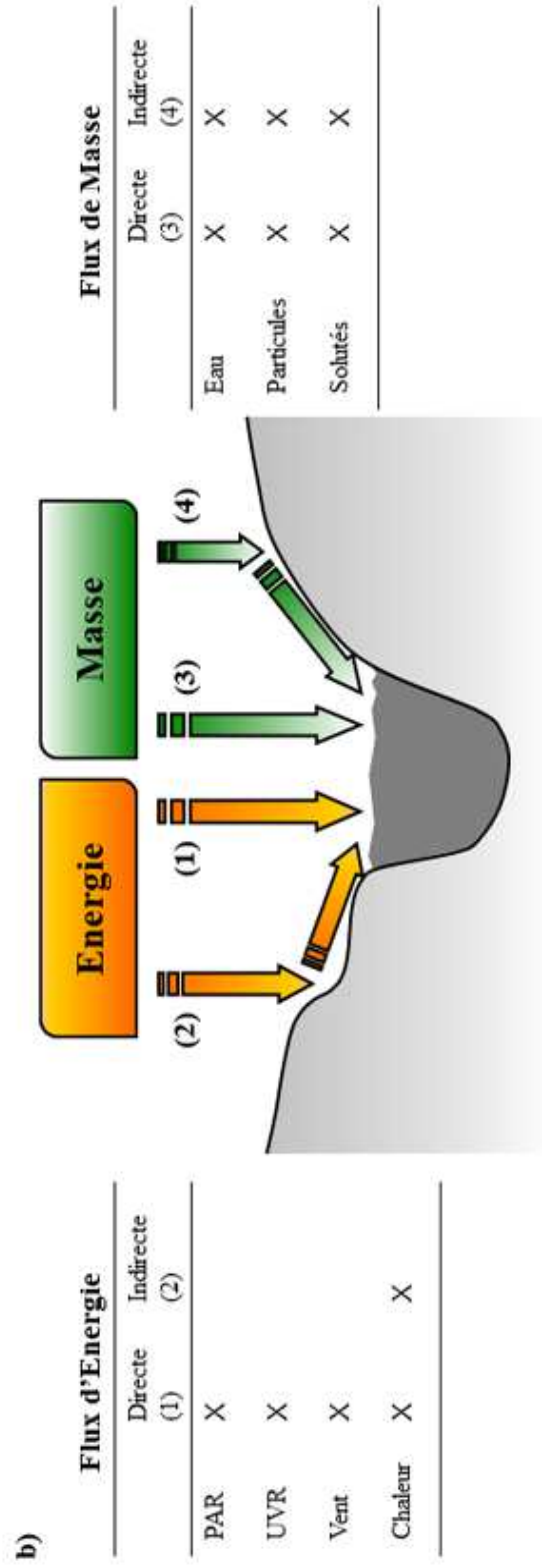
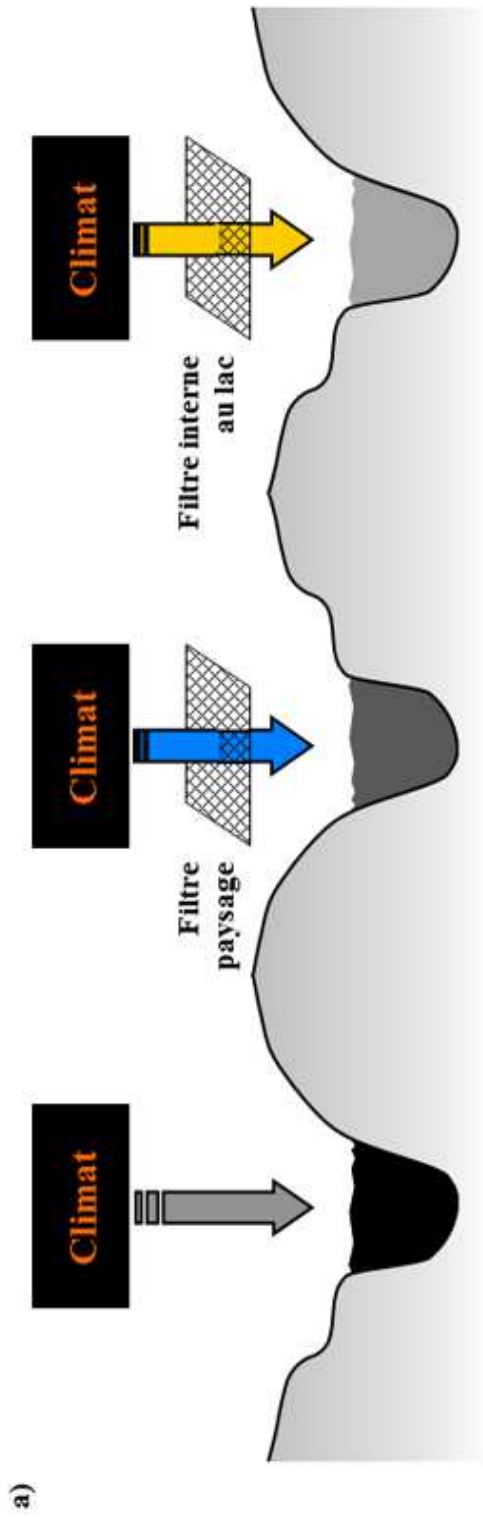
Dans cinq lacs en Laponie Finlandaise, l'accentuation de la stratification (sur le siècle dernier) liée à l'augmentation de la température conduit à une meilleure croissance des communautés planctoniques de diatomées (e.g., *Cyclotella* sp.) (Sovari et al. 2002). Les changements dans la stratification thermique de la colonne d'eau durant la période de dégel des lacs peuvent également affecter la composition chimique (e.g., alcalinité), comme observé dans six lacs de la région boréale du Canada (Schindler et al. 1996). Dans ces six lacs, le réchauffement climatique conduit également à une diminution du ratio précipitation:évaporation (Schindler et al. 1996). La diminution des précipitations conduit à une baisse des apports de carbone organique dissous (COD) du bassin versant par ruissellement et à terme à une meilleure transparence de l'eau (Schindler et al. 1996). Au contraire, dans un lac alpin autrichien, l'augmentation de la température de l'air entraîne une réduction de la surface du bassin versant couvert par la neige et donc une augmentation du taux d'érosion du sol (Koinig et al. 1998). Le transport de matériel vers le lac se trouve donc amplifié par le taux d'érosion du sol plus important (Koinig et al. 1998). De plus, le bassin versant de ce lac étant principalement formé de gneiss granitiques et de micaschistes nus (i.e., sans végétation), le matériel transporté vers le lac est donc majoritairement des cations basiques modifiant ainsi le pH et l'alcalinité (Koinig et al. 1998). La nature du matériel transporté vers les lacs peut varier selon les caractéristiques du bassin versant et avoir d'autres effets, tel que modifier l'impact du Rayonnement Ultra Violet (RUV) sur les communautés biologiques. Dans un lac subarctique canadien, les changements dans le développement de la forêt et donc dans la nature du sol, suivant un épisode de réchauffement climatique durant l'Holocène (coïncidant avec la période où la forêt occupée le maximum de surface il y a 5000-3000 ans), a augmenté le transport de COD (barrière naturelle contre la pénétration des RUV dans la colonne d'eau, Yan et al. 1996) vers le lac, diminuant ainsi l'effet délétère des RUV sur les communautés biologiques, contrairement aux périodes où la toundra dominait le bassin versant (Pienitz et Vincent 2000).

Par conséquent, si notre compréhension de l'impact des changements climatiques sur les lacs s'est considérablement améliorée grâce à de tels travaux, ceux-ci révèlent toutefois que le changement climatique peut conduire à des effets totalement contraires selon les lacs étudiés parce que l'impact du climat s'opère par différentes voies d'actions.

1.1.3. Les raisons de la complexité des réponses des lacs au changement climatique

1.1.3.1. Les caractéristiques locales des lacs comme filtre de l'impact du changement climatique

La comparaison de longues séries de données de 21 lacs dans le bouclier Canadien a montré que des lacs soumis à un forçage climatique similaire peuvent présenter des sensibilités variables (ici en terme de profondeur de mélange de la colonne d'eau) selon leurs caractéristiques morphométriques (Fee et al. 1996). Dans la continuité de ces travaux, des comparaisons de reconstructions paléohydrologiques de six petits lacs des grandes plaines d'Amérique du Nord montrent que la réponse (en terme de bilan hydrique) à la variabilité climatique était différente entre les sites, comme une conséquence de l'importance différentielle des flux de masse d'eau souterraine selon les régions et les positions géographiques des lacs (Fritz et al. 2000, Laird et al. 2003). Il semble donc que la sensibilité des lacs à l'impact de changements climatiques puisse être contrôlée, au moins en partie, par leurs caractéristiques locales. Dans ce contexte et dans une perspective de conceptualisation, un modèle pour comprendre comment et pourquoi les lacs présentent des réponses individualisées face aux changements climatiques a été développé par Blenckner (2005). Son objectif initial était d'évaluer comment les caractéristiques (environnementales, physiques, chimiques et biologiques) des systèmes lacustres peuvent influencer l'intensité et la persistance de l'impact du climat. Deux composantes ont donc été déterminées : une première composante comprenant la position géographique, les caractéristiques du bassin versant et la morphologie du lac et une seconde est caractérisée par l'histoire du lac et les interactions biotiques/abiotiques (Figure I.1a). Dans ce modèle, il est considéré que les deux composantes peuvent agir comme des "filtres" de l'effet du climat sur les lacs et que toutes les modifications de ces filtres (e.g., au travers des activités anthropiques) peuvent engendrer une réponse différente entre les lacs pour un même forçage climatique (Blenckner 2005).



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Figure I.1. (a) Schéma conceptuel montrant l'influence des caractéristiques locales d'un lac (filtre paysage et filtre interne au lac) sur l'intensité de l'impact du climat. Le dégradé de couleur (du noir vers le gris) indique une variation dans l'impact du climat sur le lac comme une fonction des filtres. Le schéma est adapté du modèle de Blenckner (2005). (b) Schéma représentant les onze voies potentiels d'action du climat sur les lacs. Les différentes voies d'actions sont groupées selon un impact lié au flux d'énergie ou au flux de masse. (1) et (2) représentent respectivement les voies d'actions directes et indirectes des flux d'énergie et (3) (4) représentent respectivement les voies d'action directes et indirectes des flux de masse.

I.1.3.2. Le climat comme une boîte noire regroupant un ensemble complexe de processus

L'observation des différentes voies d'actions du climat sur les écosystèmes et des potentielles interactions entre climat et forçages anthropiques locaux (e.g., Lotter et Birkks 1997, Hall et al. 1999, Quinlan et al. 2002, Pham et al. 2008) ont conduit à un autre développement conceptuel visant à englober l'ensemble des différentes voies d'actions potentielles de la variabilité climatique sur les lacs. Cet effort de synthèse a abouti au modèle de flux d'énergie et de masse (*Energy–mass flux framework*) de Leavitt et al. (2009). Contrairement à Blenckner (2005), Leavitt et al. (2009) ne considèrent pas les différents mécanismes par lesquels l'intensité de l'impact du climat peut être influencée mais prennent le problème dans l'autre sens. Pour cela, ils considèrent un modèle mettant en relief la complexité de l'impact du climat sur les lacs, en résumant les différents mécanismes directs et indirects par lesquels le changement climatique peut affecter les propriétés physiques, chimiques et biologiques des lacs. Ils proposent de synthétiser la variabilité climatique comme une combinaison de changements en terme d'apports d'énergie et de masse qui peuvent influencer directement les lacs ou indirectement, à travers leurs impacts sur le bassin versant (Figure I.1b). Dans leur modèle, les flux d'énergie proviennent du rayonnement solaire (PAR, RUV), du vent ou de la chaleur atmosphérique, tandis que les transferts de masse se font par des apports d'eau, de solutés et de particules. Plus précisément, au moins onze voies d'actions potentielles par lesquelles le climat peut affecter les lacs ont pu être identifiées (Figure I.1b). L'intensité relative des différentes voies d'actions par lesquels le climat affecte les lacs varierait d'un système à l'autre, en fonction des caractéristiques (ou filtres) précédemment définies par Blenckner (2005).

La validité de leur modèle a été testée au travers de l'analyse d'un grand nombre d'études paléolimnologiques traitant de la nature de l'impact des différentes voies d'actions du climat (définis dans leur modèle) sur les propriétés physiques, chimiques et biologiques des lacs (Leavitt et al. 2009).

Ainsi, ce modèle prend en compte le rôle joué par les activités anthropiques locales sur la réponse des lacs au climat ; ces interactions modulant l'intensité relative des différentes voies d'actions du climat (Leavitt et al. 2009). Par exemple, dans un lac des grandes plaines canadiennes, des suivis environnementaux relatifs aux changements climatiques (e.g., température, apport de particules au lac par les précipitations, période de gel) et aux activités anthropiques (e.g., apport P-N, superficie des terres agricoles) ont été comparés à des enregistrements sédimentaires de diatomées en utilisant une analyse de partition de la variance (VPA) (Hall et al. 1999). La VPA a montré que l'effet du climat seul (e.g., la température, apport de particules) expliquait seulement 5-15% de la variance totale dans la communauté de diatomées, alors que l'impact des activités anthropiques (qui se traduisaient principalement par des changements dans les apports en particules) expliquait jusqu'à trois fois plus de variation. La forte proportion de variance attribuable à l'interaction entre les forçages (climatiques et anthropiques) suggère également que l'effet du climat peut être contrôlé par l'effet des activités anthropiques (Hall et al. 1999). Dans ce lac, en particulier, les changements dans les apports en particules (originellement induits par le climat) étaient donc accentués par les activités anthropiques, lesquels en retour masquaient l'impact de l'augmentation de la température.

Le *Energy-mass flux framework* a donc été proposé comme une opportunité pour développer une compréhension hiérarchique de l'influence des différentes voies d'actions directes et indirectes du climat sur les lacs, suggérant ainsi son utilité comme base de travail futur (Leavitt et al. 2009). Cette compréhension hiérarchique sous-entend cependant un appui statistique poussé ainsi qu'une plus grande intégration des approches néo- et paléolimnologiques (Leavitt et al. 2009). Des méthodes de statistiques multivariées, telles que la VPA, ont déjà été appliquées à des études paléolimnologiques (voir McGowan et Leavitt 2009 pour des exemples) ainsi qu'à des études combinant néo- et paléolimnologie (e.g., Lotter et Birks 1997, Quinlan et al. 2002).

Mais l'un des inconvénients de la VPA est que c'est une méthode canonique basée sur la covariance entre les variables prédictives et réponses sur l'ensemble de la durée d'étude, alors qu'un forçage environnemental peut avoir une influence forte pendant une période limitée. De nouvelles approches statistiques pour l'analyse des séries temporelles ont été développées et appliquées aux reconstructions sédimentaires, tels que les modèles additifs généralisés. Ces approches permettent de prendre en compte les variations, au cours du temps, de la contribution relative des différents forçages environnementaux sur la réponse des écosystèmes (Simpson et Anderson 2009).

1.1.3.3. Parce que les impacts climatiques interagissent avec les impacts locaux

La multiplication des forçages concomitants, d'origine anthropique et climatique, sur les lacs est un phénomène de plus en plus courant surtout dans les régions qui sont densément peuplées (MEA 2005). Par exemple, avec la croissance des populations humaines, beaucoup de lacs dans ces régions ont été sujets à une phase d'eutrophisation (comme la conséquence d'importantes charges externes en phosphore vers les lacs), suivie pour un grand nombre d'entre eux d'un processus de ré-oligotrophisation (comme la conséquence notamment de mesures de contrôle des sources ponctuelles d'apports externes en phosphore). Dans ce contexte, il semble légitime que l'une des principales préoccupations actuelles soit les conséquences de l'interaction entre les changements climatiques et dans les niveaux en nutriments (Battarbee et al. 2005, Jeppesen et al. 2010), notamment dans une perspective de restauration et de gestion durable des lacs (Trolle et al. 2011). Cet intérêt découle en premier lieu du fait que certains lacs s'engagent sur une trajectoire écologique inattendue avec une réponse retardée voire avortée aux réductions des apports externes en nutriments (e.g., Anderson et al. 2005, Sondergaard et al. 2007, Visconti et al. 2008). Par exemple, la productivité primaire du lac Léman a augmenté de 30% au cours des 30 dernières années alors que les concentrations en phosphore ont été divisées par cinq (Anneville et al. 2002, Tadonlélé 2010). Cet état résulterait d'une prolifération de grandes espèces de phytoplancton filamenteuses favorisées par une augmentation de la stabilité de la colonne d'eau liée aux réchauffements climatiques, masquant ainsi les effets directs de la diminution des apports externes en nutriments au lac (Anneville et al, 2002).

L'exemple du Léman illustre par conséquent que les changements climatiques et les perturbations anthropiques locales (e.g., les changements dans les niveaux en nutriments) peuvent agir sur les mêmes caractéristiques physiques, chimiques et biologiques des lacs au travers d'effets confondants (Köhler et al. 2005, Dröscher et al. 2009), inhibant ou amplifiant les effets individuels des différents forçages (Elliott et al. 2006, Horn 2003).

A un autre niveau d'intégration, les réponses biologiques des lacs au climat, même si elles sont les conséquences d'un effet physique ou chimique des perturbations, découlent également d'une action sur les réseaux trophiques (Hughes 2000). Par exemple, dans le lac Washington, durant le processus de ré-oligotrophisation, l'analyse de longues séries de données a montré que l'établissement du bloom printanier de diatomées était plus précoce qu'auparavant. Cependant, contrairement aux diatomées, aucune précocité n'a été observée pour le pic d'abondance des Daphnies (Winder et Schindler 2004). Le "mismatch" entre les dynamiques saisonnières des diatomées et de leurs consommateurs, ou découplage des relations trophiques conduisant au déclin sur le long terme des populations de Daphnies, serait une conséquence de l'effet indirect du réchauffement climatique, et notamment de l'installation plus précoce de la stratification suite aux hivers/printemps plus doux (Winder et Schindler 2004). Un découplage temporel similaire entre le bloom printanier de diatomées et le pic d'abondance de Daphnies a été observé dans le lac Müggelsee, durant sa période hyper-eutrophe (Hubert et al. 2008) et a aussi été attribué au réchauffement climatique. Dans le lac Müggelsee, cependant, et contrairement au lac Washington, ce découplage ne conduirait pas à un déclin des Daphnies. Hubert et al. (2008) supposent que le manque de concordance avec les résultats de Winder et Schindler (2004) proviendrait de la différence de statut trophique entre les deux lacs aux périodes d'études. Le plus haut statut trophique du lac Müggelsee permettrait le soutien d'une plus forte production primaire et donc minimiserait l'impact indirect du climat sur les populations de Daphnies comme observé dans le lac Washington. Ainsi, la réponse des communautés biologiques au climat serait étroitement liée à la dynamique des interactions trophiques, elles-mêmes sous le contrôle des perturbations anthropiques locales (Winder et Schindler 2004, Hubert et al. 2008).

1.1.4. Problématique abordée : réponses des lacs au changement climatique dans un contexte de perturbations multiples

En résumé, l'ensemble des connaissances acquises ces dernières décennies sur la nature et la régulation de l'impact du climat sur les lacs soulève un point essentiel : il est nécessaire de considérer le couplage entre les changements climatiques et les perturbations anthropiques locales dans notre compréhension de la réponse des écosystèmes lacustres aux forçages climatiques. Au travers de leurs activités, les populations humaines peuvent affecter la nature et l'intensité des interactions entre les différentes voies potentielles d'actions du climat ainsi que la structure des filtres de l'effet du climat. Cependant, l'implication des interactions trophiques dans le fonctionnement des lacs ainsi que dans leurs réponses biologiques face aux forçages climatiques, soulignent le besoin d'appréhender l'impact des changements climatiques sur les lacs à l'échelle de l'écosystème entier, donc au travers d'un niveau d'intégration élevé (e.g., le réseau trophique, Van der Putten et al. 2010, Woodward et al. 2011).

Mon travail doctoral se positionne dans ce contexte : il est axé sur l'approfondissement de notre compréhension de la réponse des écosystèmes lacustres à un contexte de perturbations multiples. Il s'agit plus précisément, (i) de reconstruire les trajectoires écologiques des lacs à l'échelle du siècle, (ii) de hiérarchiser l'importance relative des changements climatiques et des perturbations anthropiques locales sur la trajectoire écologique des lacs et (iii) d'évaluer comment la vulnérabilité des lacs face aux changements climatiques dépend de la nature et de l'intensité des perturbations anthropiques locales.

I.2. Stratégie du travail doctoral

I.2.1. Les sites d'étude : des lacs soumis à un contexte de perturbations multiples

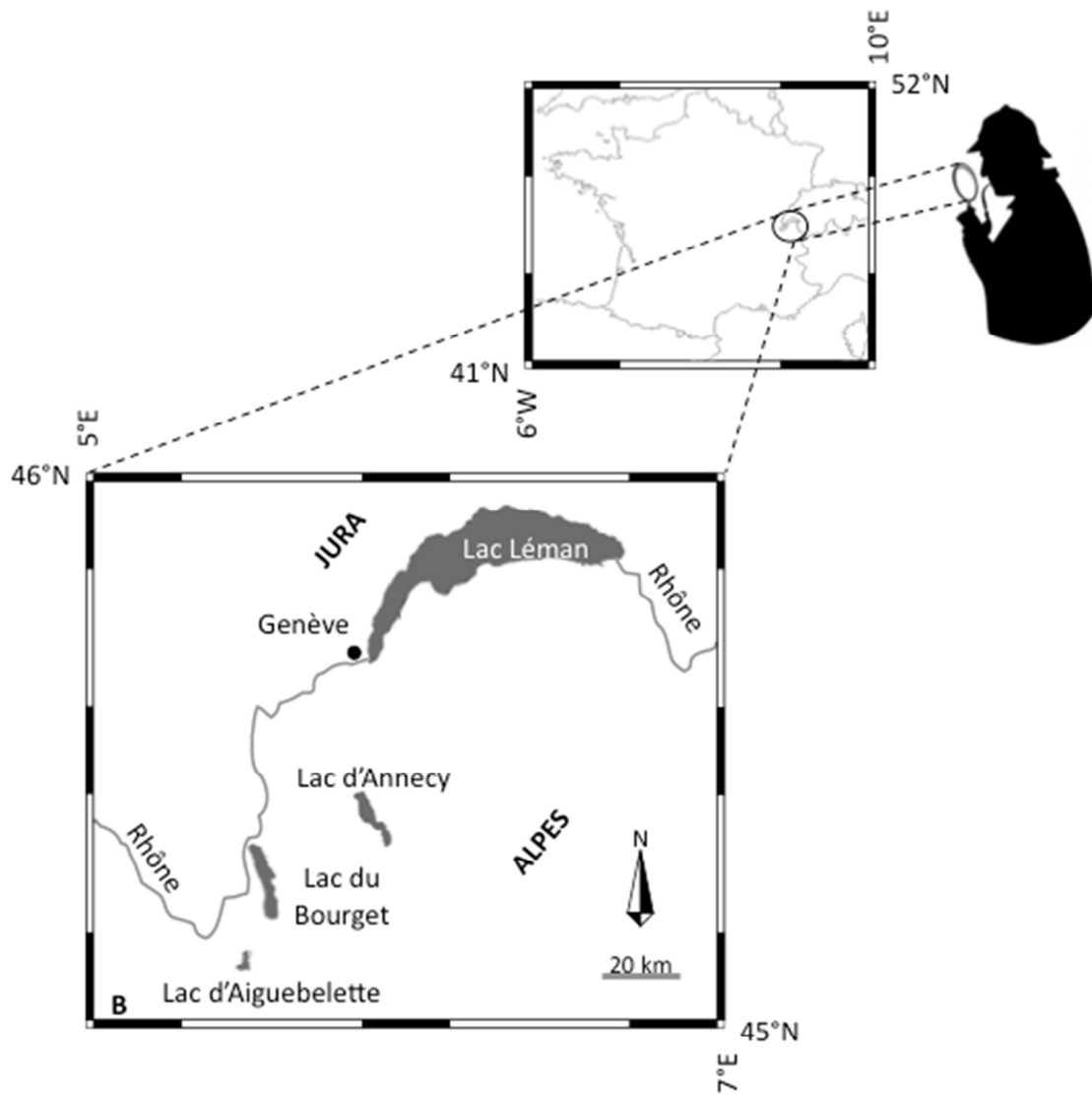
Pour aborder ces questions, nous avons concentré notre étude sur les grands lacs profonds tempérés. Notre choix s'est porté sur ce type de lacs pour plusieurs raisons :

- (i) Bien que l'amplitude des changements climatiques soit moindre en régions tempérées par rapport aux zones alpines et polaires (ACIA 2004), plusieurs études ont déjà fourni des preuves de modifications des caractéristiques physiques, chimiques et biologiques de ces lacs en réponse au climat (e.g. Weyhenmeyer et al. 1999, Straile 2000, Dokulil et al. 2010, George et al. 2010).
- (ii) Ces lacs subissent de nombreuses pressions anthropiques locales, souvent de façon concomitante aux changements climatiques (Jeppesen et al. 2005, Jeppesen et al. 2009). Deux perturbations anthropiques locales ont en particulier été considérées dans cette étude : les changements dans les apports externes en nutriments (en particulier le phosphore) et dans les pratiques de gestion piscicole, et ce, car elles sont communes à de nombreux lacs tempérés (Sas 1989, Arlinghaus et Mehner 2005). L'intérêt de ces perturbations locales vient également du fait que l'une agit essentiellement au travers d'effets ascendants ou "bottom-up" en modifiant la quantité de ressources disponibles (i.e., les changements dans les apports externes en nutriments) alors que l'autre agit au travers d'effets descendants ou "top-down", en agissant sur l'identité et la quantité des prédateurs (i.e., les changements dans les pratiques de gestion piscicole) (e.g., Lindeman 1942, Hairston et al. 1960, Hrbáček et al. 1961, Brook et Dodson 1965, Schindler 1977, Paine 1980, Carpenter et al. 1985, McQueen et al. 1986, Northcote 1988, Brett et Goldman 1997).

1.2.2. Nos objets d'étude : trois grands lacs profonds de région tempérée (le lac Léman, le lac du Bourget et le lac d'Annecy)

Les lacs Léman, du Bourget et d'Annecy sont tous localisés dans la partie Nord-Ouest des Alpes Françaises (Figure I.2). Ces trois lacs se sont formés lors de la dernière glaciation du Würm, il y a environ 19 000 ans, par le retrait des grands glaciers du Quaternaire dans le bassin molassique (Kilian 1915, Finckh et al. 1984). Leurs caractéristiques morphométriques les classent parmi les grands lacs profonds, à bassin creux et concave (Figure I.2). Ces trois lacs sont des lacs monomictiques chauds (Pourriot et Meybeck 1995), puisque les épisodes de gel total ou partiel de leur surface sont exceptionnels (e.g., 1880 pour le lac d'Annecy et le lac Léman, Forel 1880). La proximité géographique de ces lacs, avec les lacs du Bourget et d'Annecy situés respectivement à moins de 50 et 70 km du lac Léman, les place dans un contexte climatique similaire, caractérisé principalement par une augmentation globale de la température de l'air de +1.6-1.7°C depuis la fin des années 1980 (HISTALP, Auer et al. 2007). Les trois lacs font actuellement l'objet de suivi de la qualité des eaux qui ont commencé en 1957 pour le lac Léman (géré par la Commission Internationale pour la Protection des Eaux du Léman et l'INRA), en 1996 pour le lac d'Annecy (géré par le Syndicat Mixte du Lac d'Annecy et l'INRA) et en 2004 pour le lac du Bourget (géré par le Comité Intersyndical pour l'Assainissement du Lac du Bourget et l'INRA). Actuellement, ces suivis se font également dans le cadre du Système d'Observation et d'Expérimentation au long terme pour la Recherche en Environnement (SOERE).

Comme beaucoup de lacs dans les pays industrialisés, l'augmentation des pressions anthropiques au cours du développement démographique et économique (marqué par une forte intensification dans les années 1930-40) a conduit à une augmentation significative des concentrations en phosphore dans les trois lacs, conduisant à l'observation de symptômes d'eutrophisation (Druart et Pelletier 1998, Anneville et al. 2002, Giguet-Covex et al. 2010, Perga et al. 2010) d'intensité variable entre les trois lacs. Initialement classé comme ultra-oligotrophe, le lac d'Annecy a évolué vers un statut oligo-mésotrophe à la fin des années 1960 (avec une concentration maximale en phosphore total ([TP]) $< 20 \mu\text{gP L}^{-1}$) (Perga et al. 2010). L'eutrophisation du lac d'Annecy est restée modérée grâce à la mise en place précoce, dès 1967, de contrôle des apports en nutriments par la construction d'un collecteur des eaux usées autour du lac.



Lacs	Z_{\max}^a (m)	Z_{moy}^b (m)	Alt ^c (m)	A_L^d (Km ²)	OI ^e	(Vd ⁻¹) ^f
Léman	309	152	372	582	6.301	0.678
Bourget	145	80	232	42	12.344	0.604
Annecy	69	40	447	27	7.698	0.575
Aiguebelette	70	31	373	5.45	13.360	0.74

←

Figure I.2. Localisation géographique et caractéristiques morphométriques des trois lacs d'étude.

^a Z_{\max} : profondeur maximale du lac (en m)

^b Z_{moy} : profondeur moyenne du lac (en m)

^c Alt: altitude (en m)

^d A_L : surface du lac (en km^2)

^e OI: Indice de Osgood définit comme $Z_{\text{moy}}/A_L^{0.5}$ (Z_{moy} en m et A_L en Km^2). Cet indice permet de classer les lacs selon la morphométrie du bassin lacustre et plus précisément le creux du bassin qui peut influencer l'intensité du mélange de la colonne d'eau induit par le vent (Meybeck 1995). Lac très plat, $\text{OI} < 0.1$; lac plat, $0.1 < \text{OI} < 0.5$; lac normal, $0.5 < \text{OI} < 2.5$; lac creux, $2.5 < \text{OI} < 12.5$; lac très creux, $\text{OI} > 12.5$.

^f V_d^{-1} : facteur de forme du lac définit comme $Z_{\max}/3*Z_{\text{moy}}$. Ce facteur de forme permet de classer les lacs selon la forme du lac et les conditions de pente qui influencent la distribution des zones d'érosion, de transport et d'accumulation comme déterminé à partir de la courbe hypsographique (Håkanson et Jansson 1983). Très convexe, $3.0 \leq V_d^{-1} < 20$; convexe, $1.5 \leq V_d^{-1} < 3.0$; légèrement convexe, $1.0 \leq V_d^{-1} < 1.5$; linéaire, $0.75 \leq V_d^{-1} < 1.0$; concave, $0.5 \leq V_d^{-1} < 0.75$.

Depuis, la [TP] est en baisse constante, atteignant aujourd'hui des valeurs $< 6 \mu\text{gP L}^{-1}$. A l'inverse, les mesures de remédiation ont été beaucoup plus tardives dans les lacs Léman et du Bourget (fin des années 1970 début des années 1980) alors que les deux lacs avaient déjà évolué d'un statut oligotrophe à eutrophe (avec des [TP] maximales de 90 et 130 $\mu\text{gP L}^{-1}$ respectivement pour le lac Léman et le lac du Bourget). Depuis, la mise en place de stations d'épuration et les interdictions de détergents phosphatés ont permis de réduire significativement les [TP] des deux lacs jusqu'à des valeurs plus typiques de lacs oligo-mésotrophes (23 et 17 $\mu\text{gP L}^{-1}$ en 2010 respectivement pour le lac Léman et du Bourget, INRA Systèmes d'Observation et d'Expérimentation pour la Recherche en Environnement).

La pêche représentant une importante activité économique et de loisirs, les lacs Léman, du Bourget et d'Annecy sont aussi soumis à des pressions d'origine anthropique sur les populations piscicoles. Les communautés piscicoles y sont similaires et typiques de lacs péri-alpins [i.e., le corégone (*Coregonus lavaretus*), l'omble chevalier (*Salvelinus alpinus*), la truite (*Salmo trutta lacustris*), le brochet (*Esox lucius*), la perche (*Perca fluviatilis*), la lotte (*Lota lota*) et le gardon (*Rutilus rutilus*), Gerdeaux et al. 2006]. Parmi ces espèces de poissons, le corégone qui est essentiellement zooplanctonophage dans les lacs péri-alpins (Berg et al. 1994, Perga et Gerdeaux 2005) est l'une des principales ressources halieutiques. Originellement autochtone dans les lacs Léman et du Bourget, le corégone a été introduit en 1886 dans le lac d'Annecy (Le Roux 1908). Dans le lac Léman, cependant, la surexploitation des deux espèces indigènes de corégone a conduit à leur disparition à la fin du 19^{ème} siècle.

Par la suite, le corégone a été réintroduit (dès 1922) à partir d'individus du lac du Bourget et du lac de Neuchâtel (Dottrens 1950, Keith et Allardi 2001). Dans ces lacs, le repeuplement de corégone est une pratique courante pour soutenir le recrutement exercé par l'activité de pêche (Champigneulle et al. 2001, Gerdeaux et al. 2006). Dans le lac d'Annecy, le repeuplement de corégone était sporadique de 1900 à 1930, puis annuel de 1936 à 1997, tandis que dans le lac Léman, le repeuplement est annuel depuis 1970. Dans le lac du Bourget, le repeuplement de corégone était annuel de 1943 à 1965, puis à nouveau de 1986 à 2008 (Champigneulle et al. 2001). Les pratiques de gestion piscicole, axées en particulier sur cette espèce, peuvent générer des effets en cascade sur les autres compartiments du réseau trophique pélagique.

Un quatrième lac, le lac d'Aiguebelette, a également été utilisé comme objet d'étude. Son origine de formation et ses caractéristiques morphométriques communes avec les trois autres lacs (Figure I.2) ainsi que sa localisation géographique en font un bon système pour aborder une question méthodologique centrale de ce travail (cf., I.3.1 et chapitre II), dont l'objectif est de valider notre démarche scientifique. En effet, le lac d'Aiguebelette présente la caractéristique d'être relativement bien protégé du vent, permettant la mise en place, sur une année entière, du dispositif expérimental nécessaire à cette question méthodologique.

1.2.3. Notre démarche scientifique : une approche rétrospective “la paléolimnologie” pour une vision sur le long terme

Si les lacs Léman, du Bourget et d'Annecy font l'objet de suivis instrumentaux, la couverture de ces suivis ne permet pas une reconstruction sur le long terme. D'un autre côté, les caractéristiques structurales de leurs sédiments peuvent s'avérer d'une grande importance pour les reconstructions paléolimnologiques. Dans de nombreux cas, en déclenchant une baisse drastique des concentrations en oxygène dans les eaux profondes des lacs, l'eutrophisation favorise un dépôt sédimentaire laminé annuellement (i.e., varves biochimiques) (Goslar et al. 1999, de Vincent et al. 2006). De tels dépôts sédimentaires laminés annuellement ont été observés dans les trois lacs (Span et al. 1992, Nomade 2005, Giguet-Covex et al. 2010) avec une apparition correspondant approximativement aux périodes respectives de début d'eutrophisation (Giguet-Covex et al. 2010).

L'utilisation des dépôts laminés couplée avec des méthodes de radiochronologies permettent d'obtenir une datation à haute résolution (i.e., pouvant aller jusqu'à une résolution annuelle, voire saisonnière) des sédiments lacustres des trois lacs (Giguet-Covex et al. 2010). Une datation des sédiments peut être obtenue en déterminant la distribution de radionucléides le long de carottes sédimentaires. L'une des méthodes les plus largement utilisées pour la datation relative des sédiments est la mesure du $^{210}\text{Pb}_{\text{exc}}$ ($T_{1/2} = 22.3$ ans) qui permet d'obtenir une relation âge-profondeur relativement fiable sur les 100-150 dernières années (Noller 2000). Mais, malgré plusieurs améliorations, cette méthode basée sur des flux de ^{210}Pb et de sédiments constants ainsi qu'une position statique des radionucléides ne conduit pas toujours à des âges précis (Appleby et al. 1991). Cette méthode a donc été couplée à la mesure de radionucléides artificiels, ^{137}Cs et ^{241}Am , qui permettent la datation absolue et sans ambiguïté d'un ou deux événements (i.e., l'accident de Tchernobyl en 1986 avec un pic de ^{137}Cs et le maximum de retombées des essais atmosphériques d'armes nucléaires en 1963 avec de fortes activités de ^{137}Cs et de ^{241}Am) (Appleby 2000). Un troisième radioélément, le ^7Be qui est un radionucléide cosmogénique ($T_{1/2} = 53.3$ jours), a été utilisé pour vérifier si les sommets des carottes sédimentaires correspondaient à l'interface eau-sédiment en mesurant la remobilisation des sédiments (Krishnaswami et al. 1980, Sharma et al. 1987). L'activité des radionucléides (^{210}Pb , ^{137}Cs et ^{241}Am) a été mesurée par spectrométrie gamma au laboratoire souterrain de Modane (Reyss et al. 1995) et les modèles d'âge et de datation des carottes utilisés dans cette thèse ont été construits par Jean-Louis Reyss (LSCE), Fanien Arnaud, Jean-Philippe Jenny, Cécile Pignol et Pierre Sabatier (EDYTEM).

1.2.4. Notre modèle d'étude : les cladocères comme le trépied gagnant pour l'étude de la réponse des lacs aux changements sur le long terme

Une grande majorité des études paléolimnologiques traitant de la réponse des lacs aux forçages environnementaux s'est focalisée principalement sur les producteurs primaires, et notamment les diatomées. L'une des raisons est que les changements climatiques et dans les apports externes en nutriments affectent la quantité de lumière incidente, la température de l'eau, la turbidité, la concentration en nutriments, les interactions trophiques et donc, directement la communauté phytoplanctonique (Harris 1986).

Parmi l'ensemble des micro-algues, les diatomées sont non seulement parmi celles qui montrent de fortes variations taxonomiques en fonction des conditions environnementales précédemment mentionnées (Smol et al. 2001a), mais aussi celles qui génèrent des restes fossiles archivés dans les sédiments (i.e., les frustules) (Wolin et al. 1988).

D'autres organismes biologiques, telles que les larves de chironomes, ont également montré une certaine prédisposition, par exemple, pour les reconstructions quantitatives des changements de température, du niveau des lacs, du processus d'acidification et de la formation d'anoxie hypolimnétique liée au processus d'eutrophisation (e.g., Walker 1987, Hofmann 1988, Walker 2001, Millet et al. 2010, Verbruggen 2010).

Par rapport aux groupes taxonomiques précédemment cités, le zooplancton a été beaucoup plus rarement utilisé pour les reconstructions paléo-environnementales. Cependant, trois propriétés principales du zooplancton, et en particulier des cladocères, en font le compartiment biologique le plus apte à répondre aux objectifs de cette thèse.

1.2.4.1. Les assemblages fossiles de cladocères et leur face cachée

Les restes chitineux d'exosquelettes de zooplancton sont généralement abondants dans les sédiments lacustres (Frey 1986, Hann 1988). Les fragments d'exosquelettes à l'origine des restes fossiles sont issus de la mort ou des mues des individus. A la mort ou à la mue d'un individu, des processus mécaniques, chimiques et biologiques dans les lacs désarticulent, fragmentent et décomposent les restes de zooplancton avant leur enfouissement dans les sédiments (Kerfoot 1995, Kattel 2009). Tous les taxons du zooplancton ne présentent pourtant pas la même sensibilité face à ces processus. Les copépodes et les rotifères en particulier sont rarement représentés dans les assemblages fossiles (Rautio et al. 2000) ; seuls leurs œufs sont occasionnellement analysés dans les sédiments pour inférer, de façon qualitative plus que quantitative, leur présence historique (e.g., Knapp et al. 2001, van Geel 2001). A l'inverse, les cladocères sont bien préservés, même si cette préservation diffère selon les parties corporelles et les taxons (Hann 1988). Alors que les Bosminidae et les Chydoridae sont représentés au travers de capsules céphaliques, de carapaces et de postabdomens, seulement les griffes postabdominales, les mandibules, les segments d'exopodites ou des fragments de carapace sont retrouvés pour les Daphniidae, les Sididae, les Holopedidae et les Macrothricidae (Szeroczynska et Sarmaja-Korjonen 2007).

Les Leptodoridae, les Polyphemidae et les Cercopagidae sont représentés par des mandibules et des furcas caudales (Szeroczynska et Sarmaja-Korjonen 2007). Les cladocères présentent une parthénogénèse cyclique, c'est-à-dire que la reproduction des individus s'opère, la plupart du temps, par multiplication clonale, conduisant à la libération directe de leurs descendants. Les plus rares épisodes de reproduction sexuée génèrent cependant des éhippies ou œufs de dormance qui sont identifiables et relativement bien préservés dans les sédiments (Vandekerkhove et al. 2004). Ainsi, les modifications de structure des communautés de cladocères et éventuellement des stratégies de reproduction peuvent être aisément reconstruites à partir des archives sédimentaires.

1.2.4.2. Leur position trophique comme un intégrateur des modifications du réseau trophique pélagique lacustre

La dynamique des réseaux trophiques est fortement régulée par l'effet des contrôles "bottom-up" et "top-down" (e.g., Carpenter et al. 1985, Pinel-Alloul et al. 1998, Carpenter et al. 2001, Benndorf et al. 2002). Rappelons, toutefois, que les deux perturbations locales considérées ici, les changements dans les apports en nutriments et dans les pratiques de gestion piscicole, agissent respectivement au travers d'effets "bottom-up" et "top-down". Le climat, quant à lui, peut affecter la dynamique des réseaux trophiques au travers de modifications, à la fois, des effets du contrôle "bottom-up" et "top-down" (Jeppesen et al. 2007, Jeppesen et al. 2009). De plus, il a été montré que les effets du contrôle "top-down" sont censés être plus forts pour les niveaux trophiques supérieurs et s'estomper au travers de la chaîne trophique vers les niveaux inférieurs, avec la réciproque qui est vraie pour le contrôle "bottom-up" (McQueen et al. 1986, 1989). Or, les cladocères occupent, comme consommateurs primaires et proies de choix pour les poissons, une position centrale dans les réseaux trophiques pélagiques lacustres, comme lien dans les flux d'énergie entre la base des chaînes trophiques et les prédateurs supérieurs (e.g., Lehman 1980, Kerfoot 1987, Jürgens et al. 1994). Ainsi, contrairement aux producteurs primaires, la dynamique de leur population (en termes d'abondance et de composition spécifique) répondrait, de façon intégrée, à l'ensemble des modifications des contrôles ascendants et descendants sur le réseau trophique pélagique issu des perturbations anthropiques locales et régionales.

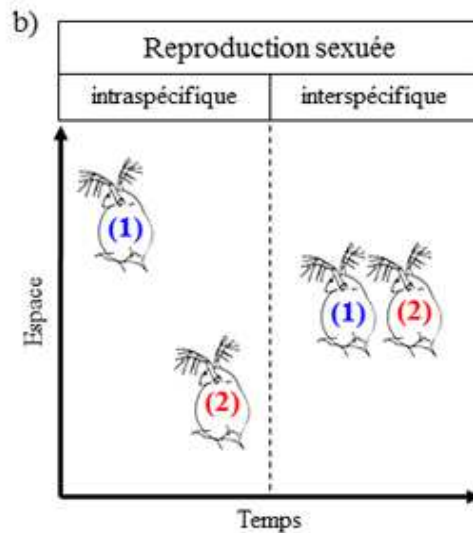
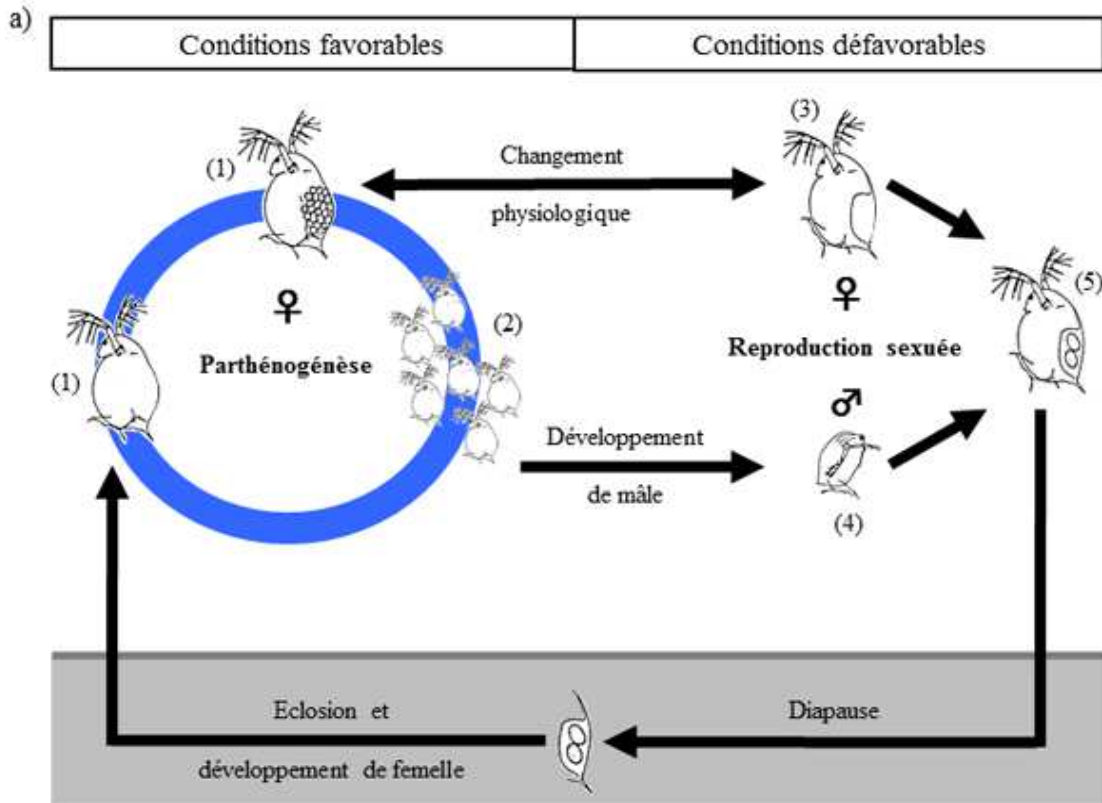


Figure I.3. (a) Cycle de reproduction des Daphnies. Durant les conditions favorables, les Daphnies se reproduisent par parthénogénèse. Lorsque les conditions deviennent défavorables, les Daphnies basculent sur une reproduction sexuée. Les numéros correspondent aux différents stades reproductifs : (1) femelle parthénogénétique, (2) descendance asexuée, (3) femelle sexuée, (4) mâle, (5) femelle sexuée avec éphippie. (b) Reproduction intra- et interspécifique ; partie de gauche : condition de reproduction sexuée de deux espèces syntopiques avec une séparation spatiale et temporelle, partie de droite : conditions de chevauchement spatial et temporel dans l'induction de la reproduction sexuée de deux espèces syntopiques conduisant à une hybridation.

I.2.4.3. Les éhippies : une banque d'ADN fossile

Le basculement d'une reproduction parthénogénétique vers une reproduction sexuée chez les cladocères est considéré comme une stratégie adaptative en réponse aux perturbations environnementales (Hebert 1978). En effet, l'induction de la reproduction sexuée est restreinte à des fenêtres de temps où les conditions environnementales sont défavorables tels que des changements dans la température, la photopériode et le niveau de ressource alimentaire (Stross et Hill 1965, Hobaek et Larsson 1990, Kleiven et al. 1992) aussi bien que des changements dans l'intensité du contrôle descendant des communautés piscicoles (Slusarczyk 1995, Pijanowska et Slope 1996, Slusarczyk 2001). Lors de la reproduction sexuée, des femelles sexuées et des mâles sont formés (Figure I.3) (Hebert 1978). Les femelles sexuées produisent généralement deux œufs méiotiques haploïdes qui nécessitent d'être fertilisés (De Meester et al. 2004). Après leur fertilisation, ces œufs sont encapsulés dans une structure appelée éhippie et rentrent en diapause. Les éhippies sont constituées de deux valves chitineuses sécrétées autour de la poche incubatrice des femelles à partir de leur carapace (Schultz 1977). La structure protectrice des éhippies permet aux œufs de survivre aux conditions environnementales défavorables (Cáceres 1998, Mellors 1975) pour éclore lorsque les conditions environnementales redeviennent favorables (Brendonk et De Meester 2003). Bien que les processus d'éclosion ne soient pas totalement compris, l'augmentation de la température et la photopériode peuvent jouer un rôle dans l'arrêt de la diapause des œufs (Schwartz et Hebert 1987). Généralement, toutes les éhippies n'éclosent pas, ce qui entraîne l'accumulation d'une banque d'éhippies dans les sédiments (De Statio 1989, Cáceres et Hairston 1998, Brendonk et De Meester 2003). De plus, les œufs contenus dans des éhippies âgées d'une centaine d'années peuvent être viables indiquant une préservation de l'ADN (Hairston et al. 1995, Brendonk et De Meester 2003). Les éhippies archivées dans des sédiments lacustres laminés peuvent donc renfermer de l'ADN d'assez bonne qualité pour déterminer l'architecture génétique des banques d'éhippies. Ainsi, la détermination de l'architecture génétique des banques d'éhippies permettrait d'identifier les espèces qui ont eu recours à la reproduction sexuée au cours du temps. Dans nos lacs, les banques d'éhippies sont principalement constituées par les éhippies des Daphnies du complexe d'espèces *Daphnia longispina*. Notre étude c'est donc focalisée sur ce type d'éhippie.

I.3. Structure de la thèse

Les travaux réalisés durant cette thèse sont présentés sous forme de trois volets. Un premier volet, plus méthodologique, s'attache à approfondir nos connaissances sur la représentativité des communautés sources de cladocères par les assemblages de restes. Le second aborde la réponse des communautés de cladocères pélagiques à l'impact des trois perturbations environnementales considérées dans cette étude sur les réseaux trophiques pélagiques. Pour finir, le troisième volet, plus spécifiquement consacré aux populations de Daphnies, traite de l'impact des trois perturbations environnementales sur leurs stratégies de reproduction.

I.3.1. Volet 1 : Les restes fossiles de cladocères et leur représentativité

Habituellement, les reconstructions paléolimnologiques basées sur le comptage et la détermination spécifique des restes fossiles de cladocères reposent sur deux hypothèses *a priori* :

- (i) les restes de cladocères représentent de façon relativement fiable les communautés sources malgré une préservation différentielle entre les taxons et les parties corporelles (comme vu précédemment) ;
- (ii) une carotte sédimentaire prélevée au centre du lac, dans la partie la plus profonde, est représentative de la communauté de cladocères du lac en entier.

La première hypothèse vient probablement du fait que des causes potentielles de la préservation différentielle entre taxons de cladocères ont été mentionnées relativement tôt (Deveey 1964) mais n'ont été que peu testées. Initialement, cette préservation différentielle était attribuée à l'épaisseur et à la structure chimique de la chitine qui varie entre les parties corporelles et les taxons de cladocères (Deveey 1964). La deuxième hypothèse découle du principe de "*funneling effect*" (Ohle 1962) selon lequel les bassins les plus profonds des lacs peuvent être considérés comme des trappes naturelles à sédiments et seraient donc représentatifs de l'ensemble du lac.

Cependant, l'archivage sédimentaire des restes fossiles d'organismes se fait sous l'influence de processus taphonomiques qui agissent comme des filtres sur l'information biologique (Behrensmeyer et Kidwell 1985, Behrensmeyer et al. 2000). D'après le concept originel de la taphonomie établi par Efremov (1940), Behrensmeyer et Kidwell (1985) définissent les processus taphonomiques comme tous les processus affectant la préservation des fossiles, de leur formation (i.e., à la mort ou à la perte d'une partie corporelle d'un individu) jusqu'à leur découverte par les paléoécologistes. La découverte par les paléoécologistes sous-entend la collecte, la préparation et l'analyse d'échantillons (Behrensmeyer et Kidwell 1985, Behrensmeyer et al. 2000). Cependant, les processus taphonomiques ne sont que trop rarement pris en considération dans les reconstructions paléo-écologiques alors qu'une meilleure compréhension de ceux-ci permettraient une plus grande fiabilité de l'interprétation des archives sédimentaires (Behrensmeyer et Kidwell 1985, Kidwell et Behrensmeyer 1988, Cohen 2003a).

Toutefois, des études ont essayé d'investir les limites des deux hypothèses précédemment citées en se focalisant sur les biais taphonomiques potentiels. Dans l'ensemble, ces études ont amélioré notre compréhension du potentiel et des limites de la représentativité des assemblages fossiles de cladocères. Tout d'abord, la préservation différentielle entre les taxons de cladocères pourrait être un artefact et serait le reflet de taux de mues spécifiques entre les taxons, lesquels contrôlent les quantités de restes libérés dans le milieu et donc la quantité de restes qui sédimentent (Kerfoot 1981, Kerfoot 1995). Cette préservation différentielle pourrait également être le résultat de la préparation et de l'analyse des échantillons, lesquelles seraient désavantageuses notamment pour les griffes postabdominales de cladocères (Sarmaja-Korjonen 2007 et Nykänen et al. 2009). Ensuite, la composition des assemblages fossiles des zones profondes dépendrait de la distribution spatiale des communautés de cladocères littorales et pélagiques ainsi que des processus de sédimentation (e.g., Müller 1964, Whiteside et Harmsworth 1967, Hofmann 1987, Kattal et al. 2007), lesquels sont étroitement liés à la morphométrie des bassins lacustres (e.g., Lehman 1975, Håkanson 1981, Håkanson et Jansson 1983, Hilton et al. 1986).

Malgré ces observations, notre compréhension de la représentativité des assemblages fossiles de cladocères reste encore limitée et ceci pourrait considérablement restreindre la portée des résultats des reconstructions paléo-écologiques du volet 2.

Premièrement, les études des processus taphonomiques et de la représentativité des assemblages fossiles ont été réalisées principalement dans des lacs petits ou plats (mais voir Kerfoot 1995, Manca et al. 2007 pour des exemples de grands lacs profonds). Or, la morphométrie et l'hydrodynamisme diffèrent dans les petits lacs et les lacs plats par rapport aux grands lacs profonds (Wetzel 2001). La compréhension des patterns de sédimentation à un site de carottage ainsi que des limites de représentation des assemblages fossiles dans les grands lacs profonds est donc cruciale pour l'interprétation des reconstructions paléolimnologiques des volets 2 et 3 de cette thèse.

De plus, la majorité des investigations taphonomiques sur les restes de cladocères s'est principalement focalisée sur la fidélité taxonomique des assemblages fossiles (i.e., quelles sont les espèces représentées dans les assemblages fossiles ?) et la fidélité spatiale (i.e., quelle est l'échelle spatiale de répartition des restes ?) (e.g., Deevey 1964, Rautio et al. 2000, Kattal et al. 2007). La résolution temporelle des dépôts sédimentaires (i.e., la sédimentation est-elle continue ou épisodique sur une année ?) a rarement été considérée (voir Kerfoot 1995, Nykänen et al. 2009) alors que les reconstructions paléolimnologiques du volet 2 sont réalisées à haute résolution temporelle (i.e., datation annuelle).

Enfin, l'un de nos objectifs est d'étudier l'impact des changements dans les pratiques de gestion piscicole (qui agit au travers d'effet "top-down") sur la structure des communautés de cladocères. Si la taille des restes fossiles de cladocères a déjà été utilisée pour reconstruire les changements passés dans la pression de prédation et la structure des réseaux trophiques (e.g., Alexander et Hotchkiss 2010, Korosi et al. 2010, Perga et al. 2010, Buchaca et al. 2011), sa représentativité n'a reçu que très peu de considération jusque là (mais voir Kerfoot 1981).

Le chapitre II a donc pour objectif de palier ces limites de notre compréhension de la représentativité des assemblages de restes de cladocères en comparant, sur une échelle annuelle, la composition taxonomique et la structure en taille des communautés sources et de leurs assemblages de restes respectifs dans le lac d'Aiguebelette un grand lac profond (Figure I.1). Cette étude se focalise principalement sur l'impact des processus taphonomiques durant la sédimentation des restes le long de la colonne d'eau.

1.3.2. Volet 2 : Le rôle structurant des forçages environnementaux sur les communautés de cladocères

Les nombreux travaux expérimentaux et de suivis réalisés depuis les années 60 sur les processus de régulation des réseaux trophiques (e.g., Brooks et Dodson 1965, Lynch 1979, DeMott et Kerfoot 1982, Sommer et al. 1986, Vanni 1987, Gliwicz 2002) permettent d'énoncer des hypothèses claires sur l'impact supposé des deux perturbations locales considérées sur les assemblages de cladocères. La taille corporelle des individus est considérée comme l'une des plus importantes caractéristiques du rôle de la dynamique des assemblages de zooplancton dans les processus lacustres. L'importance de la taille est explicite dans la *size-efficiency hypothesis* (Brooks et Dodson 1965) qui postule que la dynamique des communautés de zooplancton peut être expliquée par l'équilibre entre la compétition pour la ressource et la pression de prédation. Brooks et Dodson (1965) suggèrent donc que la compétition pour la ressource induirait un déplacement de la communauté de zooplancton vers des espèces de grande taille (e.g., les Daphnies), alors que la prédation par les poissons zooplanctonophages résulterait dans un déplacement vers des espèces de petite taille (e.g., les Bosmines, les rotifères). Cette hypothèse a été renforcée au travers du modèle PEG (Plankton Ecology Group, Sommer et al. 1986) et d'autres études montrant que les changements en taille du zooplancton pouvaient modifier la composition du phytoplancton (Carpenter et Kitchell 1984, Sarnelle 2005). Par conséquent, avec l'augmentation des apports en nutriments, la plus forte production primaire résulterait en une augmentation de l'abondance du zooplancton (McCauley et Klaff 1981, Hanson et Peters 1984), et en particulier des espèces de grande taille telles que les Daphnies, en l'absence de poissons planctonophages (Figure I.4) (Brooks et Dodson 1965, DeMott et Kerfoot 1982).

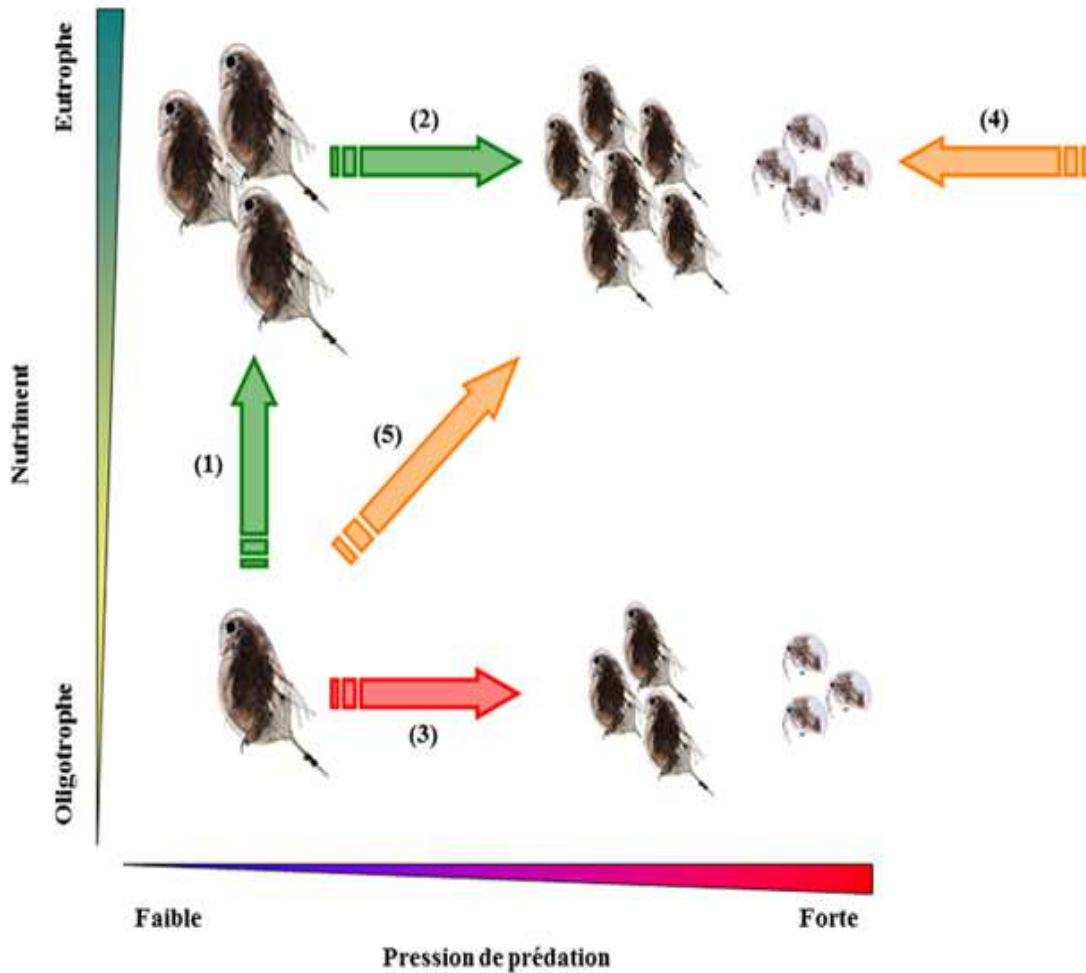


Figure I.4. Schéma conceptuel représentant nos hypothèses de travail sur l'impact potentiel des trois perturbations sur le contrôle bottom-up et top-down sur les communautés de cladocères pélagiques. (1) impact direct de l'augmentation des concentrations en nutriments sur l'abondance des cladocères, (2) impact indirect de l'augmentation des concentrations en nutriments sur les communautés de cladocères au travers d'une intensification du contrôle top-down par les poissons planctonophages, (3) impact direct de l'augmentation de l'impact descendant des poissons sur la structure en taille des cladocères, (4) impact direct du réchauffement climatique au travers des processus physiologiques, et (5) impact indirect du réchauffement climatique au travers de modification des interactions trophiques.

Les Daphnies ont un avantage compétitif sur les espèces de plus petite taille (e.g., les Bosmines) (Vanni 1986) se traduisant par un plus fort taux de filtration par individu, une plus large gamme de taille de particules ingérables, une plus faible demande métabolique par unité de masse et une meilleure résistance au faible niveau en ressource (e.g., Burns 1968, Goulden et al. 1978, Gliwicz 1980, Peters et Downing 1984, Gliwicz 1990). Cependant, lorsque la disponibilité en nutriments augmente fortement, des espèces de phytoplancton coloniales et filamenteuses et même des espèces toxiques de cyanobactéries augmentent en abondance (Vincent 1989, Watson 1997). Cette morphologie filamenteuse leur confère une résistance à la prédation et interfère avec les mécanismes de collecte de nourriture des espèces de zooplancton de grande taille (e.g., les Daphnies) plus qu'avec ceux des espèces de plus petite taille (e.g., les Bosmines) (Webster et Peters 1978, Lampert 1978), qui présentent un mode d'alimentation plus sélectif (DeMott et Dodson 1982). Sous des conditions très eutrophes, les espèces de grande taille peuvent donc perdre de leur avantage compétitif (Gliwicz et Lampert 1990, Rothhaupt 1990).

L'avantage compétitif des espèces de grande taille (e.g., les Daphnies) est souvent perdu en présence de poissons planctonophages (Hanazato et Yasumo 1989). La prédation est perçue comme l'un des principaux forçages régulant la structure en taille du zooplancton (Hall et al. 1976). Les poissons planctonophages avec un mode de prédation visuel, strict ou facultatif, se nourrissent selon une discrimination visuelle en sélectionnant d'une part, les espèces de plus grande taille (e.g., les Daphnies), et d'autre part, les plus grands individus dans les populations de proies (e.g., Zaret 1975, Post et McQueen 1987, O'Brien 1979, Gliwicz 2002). Le mode de prédation de ces poissons, selon la taille des proies, est lié à l'allocation optimale de temps et d'énergie dépensée pour chercher et manipuler les proies (Pyke et al. 1977). La prédation sélective selon la taille des poissons planctonophages peut donc avoir un effet structurant sur les communautés de zooplancton (Figure I.4) (Lynch 1979, Hanazato et al. 1990). Par exemple, en réduisant la taille des Daphnies (Stibor 1992), la prédation taille-sélective des poissons planctonophages pourrait indirectement réduire leur avantage compétitif pour la ressource, favorisant l'établissement d'espèces de plus petite taille moins compétitives (e.g., les Bosmines) (Vanni 1987).

Bien que la pression de prédation par les poissons planctonophages puisse avoir des effets en cascade sur les chaînes trophiques, l'intensité de son impact peut être liée au statut trophique des lacs (Carpenter et al. 2001). Une comparaison de 466 lacs de régions tempérées et arctiques, de profondeur et de statut trophique différents a montré une relation unimodale, le long d'un gradient de phosphore, de la contribution des Daphnies à la biomasse totale de cladocères (Jeppesen et al. 2003). Ils attribuent le déclin des Daphnies, pour des valeurs faibles en phosphore, à trois facteurs reliés à la pression de prédation par les poissons planctonophages. Dans les lacs avec un faible niveau en nutriments, l'influence des poissons, malgré leur faible densité (Müller et al. 2007), peut être attribuée au fait que la plus grande clarté de la colonne d'eau accentue le risque de prédation par des prédateurs visuels. De plus, lorsque la disponibilité en ressource est limitante, le taux de croissance du zooplancton est ralenti (Dahl-Hansen 1995), augmentant le temps d'exposition à la prédation. Une autre explication peut être un soutien des poissons planctonophages par la production benthique facilitant la prédation sur les grandes espèces de zooplancton pélagique (Vadebonceur et al. 2002, Vander Zanden et Vadebonceur 2002). D'autre part, avec l'augmentation du niveau en nutriments, l'abondance de cyprinidés planctonophages augmente, alors que la proportion relative de poissons piscivores diminue, affectant la structure des communautés de zooplancton au travers d'une forte pression de prédation sur les Daphnies (Figure I.4) (Olin et al. 2002, Jeppesen et al. 2010). Cependant, la contribution relative de la prédation par les poissons planctonophages dans la structuration des communautés de zooplancton serait moins intense dans les grands lacs profonds que dans les lacs peu profonds (Jeppesen et al. 1997, Jeppesen et al. 2003).

L'impact du changement climatique sur les communautés de zooplancton peut se faire selon différentes voies (Figure I.4) : (i) soit directement au travers de l'influence sur les processus biologiques/physiologiques (Moore et al. 1996), (ii) soit indirectement puisque la réponse spécifique des espèces au réchauffement climatique peut affecter le couplage phénologique des relations trophiques (Winder et Schindler 2004) conduisant à des modifications dans le réseau trophique (Moore et al. 1996, Wojtal-Frankiewicz 2012). Une comparaison de 81 lacs peu profonds européens a révélé que bien que la biomasse de zooplancton était reliée à la concentration en phosphore total quelle que soit la zone climatique, la biomasse de poissons planctonophages et le ratio poissons planctonophages:zooplancton augmentaient des lacs froids vers les lacs chauds, alors que le ratio zooplancton:Chla diminuait substantiellement (Gyllström et al. 2005).

Ces effets peuvent être interprétés comme une augmentation de la pression de prédation par les poissons planctonophages dans les lacs plus chauds par rapport aux lacs plus froids, résultant dans des effets en cascade sur le potentiel du zooplancton à réguler la communauté phytoplanctonique (Gyllström et al. 2005). Des études sur le terrain et expérimentales dans des lacs tropicaux et subtropicaux ont également montré que la prédation par les poissons et les invertébrés prédateurs était un facteur important dans la régulation de la communauté de zooplancton et de leur contrôle sur le phytoplancton (Arcifa et al. 1992, Pagano et al. 2003). Par conséquent, le climat peut contribuer à la structuration de la communauté de zooplancton en affectant le contrôle “top-down” par les poissons et en interagissant avec le niveau en nutriments (Gyllström et al. 2005, Jeppesen et al. 2010).

En s’appuyant sur les résultats du chapitre II, l’objectif du chapitre III consiste à (i) reconstruire les modifications dans les communautés de cladocères dans les lacs Léman, du Bourget et d’Annecy, au cours du dernier siècle, (ii) hiérarchiser l’influence des facteurs locaux (nutriments, prédation) et globaux (climat) sur ces trajectoires.

1.3.3. Volet 3 : Les éphippies de cladocères comme la boîte de Pandore des évènements d’hybridation interspécifique.

La présence de banques d’éphippies dans les sédiments des lacs a déjà offert la possibilité de reconstruire les changements passés dans la structure (e.g., Yan et al. 1996, Pollard et al. 2003, Mergeay et al. 2004, Mergeay et al. 2006), l’architecture génétique (e.g., Weider et al. 1997, Brede et al. 2009) et les trajectoires microévolutionnelles (e.g., Hairston et al. 1999, Kerfoot et al. 1999, Cousyn et al. 2001) des populations de Daphnies en réponse aux perturbations environnementales dans des petits lacs aussi bien que dans des grands lacs profonds. Ces études se basent sur l’hypothèse *a priori* que les banques d’éphippies archivées dans les sédiments sont une représentation fiable de l’abondance et de la composition taxonomique des communautés sources. Cependant, dans le lac Constance, un grand lac profond, il a été montré un manque de représentativité de la composition taxonomique des communautés sources de Daphnies par les banques d’éphippies (Jankowski et Straile 2003).

Ce manque de représentativité peut venir d'un investissement inégal dans la reproduction sexuée et donc dans la production d'éphippies entre les espèces de Daphnies (Cáceres 1998, Jankowski et Straile 2003, Keller et Spaak 2004). Dans les grands lacs profonds, les banques d'éphippies peuvent donc être informatives sur les changements dans le comportement de reproduction des Daphnies.

Par ailleurs, l'ensemble des stimuli environnementaux qui induisent le basculement vers une reproduction sexuée des Daphnies (cf., I.2.4.3.) peut être modifié par les perturbations locales (nutriments et prédation) et régionales (climat). Ces perturbations locales et régionales peuvent donc avoir une incidence sur les déclencheurs de la reproduction des Daphnies au cours du temps. Les modifications de l'intensité et de la durée des stimuli environnementaux peuvent affecter le comportement de reproduction à tel point que des événements d'hybridation interspécifique se produisent (Brede et al. 2009). Cependant, la nature des déclencheurs de l'hybridation interspécifique a rarement été étudiée sur le long terme. Habituellement, la présence de barrières de reproduction pré- et post-zygotiques entre des espèces syntopiques limitent l'hybridation interspécifique (Spaak 1995, Schwenk et al. 2001). En effet, l'hybridation interspécifique requiert une apparition simultanée des mâles et des femelles sexués de deux espèces (Figure I.3). Les échelles temporelles et spatiales dans l'induction de mâles et de femelles sexués de deux espèces syntopiques peuvent donc être des barrières de reproduction pré-zygotiques empêchant l'hybridation (Spaak 2004). Par conséquent, l'apparition d'évènements d'hybridation interspécifique coïncidant avec des périodes de fortes perturbations anthropiques (Brede et al. 2009, Rellstab et al. 2011) suggère que les conditions environnementales altèrent les comportements de reproduction des espèces syntopiques notamment, en diminuant les barrières de reproduction. L'une des conséquences de l'hybridation interspécifique est l'introgession (i.e., la propagation de matériel génétique d'une espèce dans le génome de l'autre espèce) qui est étroitement liée à la trajectoire de l'hybridation (i.e., si une espèce agit plus fréquemment comme la femelle sexuée ou le mâle). De plus, la trajectoire de l'hybridation et de ce fait, l'introgession, peuvent avoir des conséquences écologique et évolutive sur les communautés de Daphnies (Schwenk et Spaak 1995, Brede 2008).

Le chapitre IV a donc pour objectif d'analyser l'architecture génétique des banques d'éphippies des Daphnies dans les lacs Léman, du Bourget et d'Annecy pour (i) reconstruire les changements dans le comportement de reproduction des communautés de Daphnies, (ii) estimer le rôle des trois perturbations environnementales considérées dans l'induction simultanée de la reproduction sexuée par les espèces de Daphnies et (iii) déterminer la trajectoire de l'hybridation interspécifique.

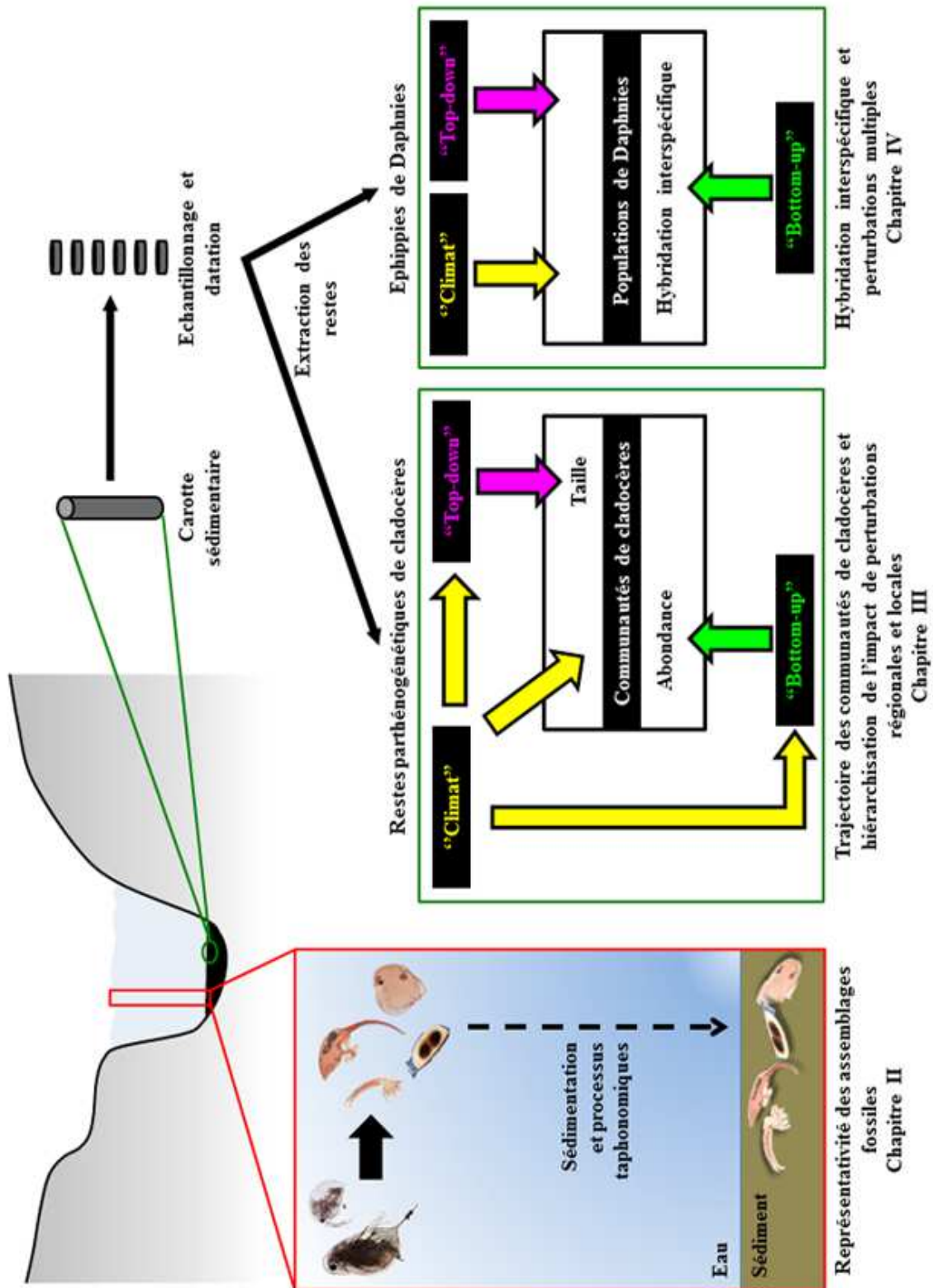


Figure I.5. Schéma récapitulatif des trois volets abordés dans cette thèse.

II. Assemblages fossiles, communautés sources et représentativité

**Effects of production, sedimentation and taphonomic processes
on the composition and size structure of sedimenting
cladoceran remains in a large deep subalpine lake:
paleo-ecological implications.
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*Keywords: Paleolimnology, Daphnia, Bosmina, sediment trap, cladoceran sub-fossil
remains, seasonal dynamics, completeness of time-series*

II.1. Abstract

Changes in the composition and size structure of cladoceran remains collected in sediment traps (ST) were compared at a monthly time-resolution to the changes in the cladoceran source communities in order to assess the effects of production, sedimentation and taphonomic processes on the composition, completeness of time series and size structure of cladoceran remains in a large deep monomictic subalpine lake. Cladoceran remains collected in the ST globally reflected seasonal changes in the composition of the source community for the dominant taxa (*Daphnia* sp., *Eubosmina* spp., and *D. brachyurum*) but failed in capturing accurately the seasonal changes in the abundance of the least abundant species, *B. longirostris*. Using allometric relationships, the average body size of the organisms that produced the remains retrieved in the ST could be reconstructed. Although the cladoceran average body size estimated from trap remains was always smaller than that of the source communities, temporal changes in the average body size of the dominant taxa in the source community were captured by trap samples. Our results showed that, in this deep subalpine lake, cladoceran remains production, sedimentation and taphonomic processes within the water column did not alter the compositional fidelity of remains at seasonal and annual time scales for the dominant taxa. Results did not show any significant over-representation of *Bosmina* and subsequent underrepresentation of *Daphnia* in contrast to previous studies on small and flat lakes. Our results suggest that the frequently observed underestimation of *Daphnia* in fossil assemblages could be a consequence of the mesh size used when processing sediment core samples rather than of varying magnitude of degradation processes between small or flat lakes and deep lakes. Finally, our results support the use of the size of cladoceran remains within paleo-ecological studies to assess past changes in the size structure of the source communities.

II.2. Introduction

Sedimentary cladoceran remains are increasingly used, alone or in combination with other paleo-indicators, to evaluate the response of lakes to various environmental stressors, such as acidification, eutrophication, biomanipulation or climate change (Jeppesen et al., 2001; Korhola & Rautio, 2001; Amsinck et al., 2007). Although the understanding of archiving processes is crucial to properly reconstruct temporal changes in cladoceran communities from their subfossil records (Frey, 1960, 1988), this issue has not been sufficiently considered. The transmission of biogenic signal from the water column to the sediment is not a simple linear relationship between production and sedimentation of biogenic remains. Therefore, the structure of fossil assemblages usually differs from their living source communities as a result of taphonomic processes acting as filters on biological information (Behrensmeyer & Kidwell, 1985; Behrensmeyer et al., 2000). Sedimentary records could hence provide a distorted picture of the source community, especially in terms of compositional and spatial fidelity (SF), temporal resolution and completeness of time series (CTS) (Kidwell & Brenchley, 1996; Behrensmeyer et al., 2000).

The few investigations dedicated to the impact of taphonomic processes on cladoceran remains have essentially focused on the compositional fidelity (CF) of fossil assemblages in sediments, comparing source communities in the lake to their corresponding fossil assemblages in surface sediment (SS), sediment cores (SC) or sediment traps (ST) (Table II.1). Because of the heterogeneity of the approaches performed, results of these studies cannot be straightforwardly compared (Table II.1). However common patterns can be highlighted. These studies consistently showed that taphonomic processes do not operate equally between zooplankton taxa (Frey, 1960; Hann et al., 1994; Rautio et al., 2000), since cladoceran exoskeletons, in contrast to copepods and rotifers, are well-preserved in lake sediments. Preservation of remains might even differ among cladoceran species with *Bosmina* and chydorid well represented by different body part (Frey, 1988) in contrast to *Daphnia* which are usually underrepresented in sediment samples compared to *Bosmina* (Frey, 1960; Kattel et al., 2007; Kattel, 2009; Nykänen et al., 2009). This underrepresentation has been interpreted as a result of poor preservation of *Daphnia* remains compared to *Bosmina* remains (Frey, 1960; Kattel et al., 2007; Kattel, 2009; Nykänen et al., 2009).

Several other sources of taphonomic biases would yet deserve deeper investigation to broaden our understanding of the picture provided by cladoceran fossil assemblages.

(i) Most of the above-mentioned studies were mainly performed on small and flat lakes (Table **II.1**), which morphometry resulted in a greater proportion of littoral habitat providing a favourable habitat for littoral cladocerans such as chydorids (Frey 1960; Hann et al., 1994; Kattel et al., 2007). In contrast, large deep lakes (Table **II.1**) are more favourable for the dynamics of planktonic cladocerans such as *Daphnia* and *Bosmina* (DeSellas et al. 2008). Since preservation is different between cladoceran species, CF of archived cladoceran remains might be different between small or flat lakes and deeper and larger lakes. In addition, lake morphometry may act on the magnitude of taphonomic biases through water depth, mixing regime, current and wave activity (Frey, 1988; Larsen & McDonald, 1993; Blais & Kalff, 1995). For instance, water depth plays a role on sediment resuspension and redeposition since turbulences are often stronger in shallower lakes (Müeller 1964; Kerfoot 1981; Kerfoot 1995). Less predominant resuspension and redeposition of sediment in deeper lakes could decrease remains exposure to decomposition agents (Kerfoot 1981). The alternative hypothesis would be that, since the sedimentation from the production to the archiving zone would take longer in large deep lakes, cladoceran remains could undergo further degradation (Poulicek & Jeuniaux, 1991; Kerfoot 1995).

(ii) Most of the previous studies have also determined the level of representativity of cladoceran fossil assemblages by comparing source and fossil communities over annual time-scale (Table **II.1**). Several reasons might have triggered this choice, such as lake annual laminations providing access to a fine resolution, low sedimentation rates or logistical problems such as ice cover hampering seasonal sampling. However, biases in CF might be related to the lack of completeness of the seasonal series archived in the sediments. The production of cladoceran remains, i.e. exuvia, arises from moulting since cladocerans grow by periodically shedding their exoskeletons at the end of each instar (Anderson, 1932). Cladoceran moulting rate is closely related to their growth dynamics, which differs between taxa and is driven by physical changes, resource availability and interactions between the species (Straile & Geller, 1998; Abrantes et al., 2006; Anneville et al., 2010). Hence, cladoceran moulting rate and the subsequent production of remains should exhibit marked seasonality differences between taxa.

In addition, the sedimentation and degradation of subfossil remains should also undergo seasonal changes, depending on environmental conditions (Hood & Meyers, 1977; Behrensmeyer et al., 2000; Kidwell, 2001). For instance, the frequency of water column mixing according to the regime of thermal stratification in lakes could delay the sedimentation of cladoceran remains and increase their exposure to degradation processes, compared to the stratification period (Kerfoot, 1981, Mieszcankin & Noryskiewicz, 2000). Lateral transport could also disturb the seasonal recording of morphological characteristics of cladoceran in sediment (Kerfoot, 1981). Therefore, the potential uncoupling of the seasonal dynamics of remains production and deposition/archiving could result in a bias in the CTS with episodicity in representation of source communities.

(iii) As mentioned above, taphonomic investigations on cladoceran remains have mainly focused on the taxonomical fidelity of fossil assemblages, i.e. which source species are represented in fossil assemblages. CF could also include the fidelity of fossil assemblages in terms of the size structure of source communities. Indeed, the size of cladoceran subfossils remains have been used to reconstruct past changes in predation and past dynamics of food webs (Alexander & Hotchkiss, 2010; Korosi et al., 2010; Perga et al., 2010) since predation by fish and invertebrate predators has a structuring effect on cladoceran size with further top-down consequences in the food webs (Brooks & Dodson, 1965; Lynch, 1979; Carpenter et al., 1985). However, no previous studies have so far investigated whether taphonomic biases could alter the recording of changes in the size structure of the cladoceran source communities.

Comparing the cladoceran source communities and remains collected in ST at a high time-resolution, this study aimed at addressing to what extent production, sedimentation and taphonomic processes occurring in the water column of a large deep clearwater subalpine lake may affect cladoceran remain assemblages, and more specifically:

- 1) Are biases in CF similar to those documented in small and flat lakes?
- 2) Are there some seasonal changes in the dynamics of remain deposition and could this affect the completeness of recorded time series?
- 3) Does the size structure of the remains reflect that of the parent community throughout the year?

Table II.1. Studies addressing the question of the representativity of cladoceran source communities by fossils assemblages.

Lake	Z _{max} , (m)	Z _{mean} ^a	A _L ^b	OI ^c	(V _d ⁻¹) ^d	Stratification	Cladoceran community type ^e	Approach ^f	Quantification ^g	Time step ^h	Mesh sieve (µm)	Investi- gated bias ⁱ	Ref ^j
Madison Lakes	22.5-8.4		14.10	2.24	0.89	Dimictic	<i>Daphnia</i> sp.	CSC/SS		Multi- annual	80	CF	1
Indiana Lakes	24.4-9.1		2.04	6.35	0.90	NS	NS	TSS		Multi- annual	250	SF	2
Frais	10.0-3.5		0.07	13.52	0.95	Dimictic	<i>Bosmina</i> sp.	CSC/ST	Exuviae production	Seasonal	NS	CF, SF	3
Paul	15.0-3.9		0.01	32.05	1.28	Dimictic	<i>Daphnia</i> sp.	CSC/ST		Annual	NS	CF	4
Tuesday	18.5-6.9		0.01	62.72	0.89	Dimictic	<i>Bosmina</i> sp.	CSC/ST		Annual	NS	CF	4
Lake 227	10.0-4.4		0.05	19.67	0.76	Dimictic	<i>Bosmina</i> sp.	CSC/SS		Annual	53	CF	5
Tuesday	18.5-6.9		0.01	62.72	0.89	Dimictic	<i>Bosmina</i> sp.	CSC/SS		Annual	NS	CF	6
Washington	65.0-33.0		88.00	3.51	0.66	Monomictic	<i>Bosmina</i> sp.	CSC/ST	Exuviae production	Week	NS	CTS, SF	7
Saanajärvi	24.0-5.1		0.70	6.10	1.57	Dimictic	<i>Daphnia</i> sp.	CSC/ST/S S		Annual	50	CF	8
Loch Coire Fionnaraich	14.5-6.6		0.09	19.67	0.80	Polymictic	<i>Bosmina</i> sp.	CSC/SS, ST/SS	Loss rate	Annual	38	CF, SF	9
Maggiore	370.0-177.0		212.50	12.14	0.70	Monomictic	<i>Bosmina</i> sp.	CSC/SC		Annual	40	CF	10
Loch Coire Fionnaraich	14.5-6.6		0.09	19.67	0.81	Polymictic	<i>Bosmina</i> sp.	ST/SS	Loss rate	Annual	38	CF	11
Vesijärvi	33.0-6.8		26.00	1.18	2.33	Dimictic	<i>Bosmina</i> sp.	CSC/SC	Exuviae production	Annual	50, 25	CF, CTS	12
Aiguebelette	70.0-31.0		5.45	13.36	0.74	Monomictic	<i>Daphnia</i> sp.	CSC/ST		Loss rate	Monthly	31	CF, CTS

Table I.1. Suite

^a Z_{\max} is maximum depth (m) and Z_{mean} is mean depth (m).

^b A_L is lake area (km²).

^c OI corresponds to Osgood Index defined as $Z_{\text{mean}}/A_L^{0.5}$ (Z_{mean} in m and A_L in km²). Osgood Index allows to classify the lakes according to the morphometry of lake basin and more specifically the hollow of the basin which influences the magnitude of the water column mixing caused by wind (Meybeck, 1995). Very flat lake, $OI < 0.1$; Flat lake, $0.1 < OI < 0.5$; Normal lake, $0.5 < OI < 2.5$; Hollow lake, $2.5 < OI < 12.5$; Very hollow lake, $OI > 12.5$.

^d V_d^{-1} corresponds to the form factor which is the inverse of the volume development (Håkanson & Jansson, 1983) and is defined as $Z_{\max}/3 \cdot Z_{\text{mean}} \cdot V_d^{-1}$ -values allow to classify the lakes according to the lake form and the slope conditions which influence the area distribution of erosion, transportation and accumulation zones as determined from the relative hypsographic curves (Håkanson & Jansson, 1983). Very Convex, $3.0 \leq V_d^{-1} < 20$; Convex, $1.5 \leq V_d^{-1} < 3.0$; Slightly convex, $1.0 \leq V_d^{-1} < 1.5$; Linear, $0.75 \leq V_d^{-1} < 1.0$; Concave, $0.5 \leq V_d^{-1} < 0.75$.

^e Cladoceran community type indicates which genus dominates the cladoceran community in the study lakes.

^f "Approach" indicates the method used to determine the representation of cladoceran fossil assemblages; either by comparison of the cladoceran source communities in the lake (CSC) with cladoceran fossil assemblages in sediment traps (ST), surface sediment (SS) and sediment core (SC), or by comparison of cladoceran fossil assemblages along a transect of surface sediment (TSS).

^g "Quantification" indicates the kind of calculations made to quantify the annual accumulation of cladoceran remains in the sediment samples ; exuviae production: quantification of the annual net accumulation of remains in the sediment in relation to production from predicted production and observed flux by applying a vertical model derived from molting and death rates (see Kerfoot (1981, 1995) for more details) and loss rate: estimation of an loss rate (%) of cladoceran remains and a subsequent representation rate allowing to quantify fossilization rate of cladoceran remains (see Kattel et al., (2007) for more details).

^h "Time step" corresponds to temporal resolution of the different comparisons.

ⁱ "Investigated" bias indicates what level the taphonomic processes may affect cladoceran community ; compositional fidelity (CF), spatial fidelity (SF) and completeness of time series (CTS).

^j 1. Frey (1960), 2. Müeller (1964), 3. Kerfoot (1981), 4. Leavitt et al. (1993), 5. Hann et al. (1994), 6. Leavitt et al. (1994), 7. Kerfoot (1995), 8. Rautio et al. (2000), 9. Kattel et al. (2007), 10. Manca et al. (2007), 11. Kattel (2009), 12. Nykänen et al. (2009), 13. this study.

NS holds for 'not specified'.

II.3. Materials and methods

II.3.1. Study site

Lake Aiguebelette is a large deep subalpine lake located at the Southern edge of the Jura chain (45°33'N, 5°48'E; Figure II.1). Maximum and average depths are 70 and 31 m, respectively. It has a 5.4 km² surface area, a 59 km² catchment area, and water residence time is approximately 3 years. It is a warm monomictic lake, with surface temperature ranging, for the study year, from 12°C in winter up to 24°C in summer. Lake Aiguebelette is oligo-mesotrophic with a current trend towards a re-oligotrophication. The lake is currently monitored weekly or every two weeks by the 'Communauté de Communes du Lac d'Aiguebelette', for physical and chemical parameters using a SeaBird[®] multiparameter probe (temperature, dissolved oxygen (O₂) and chlorophyll *a* concentrations) and for phytoplankton community composition. During the period (2009–2010) and according to temperature- and O₂-depth profiles, the lake stratified from early April to mid December and the maximum thermocline depth was 13m in summer (data not shown). The lake hypolimnion is hypoxic to anoxic for most of the year.

Due to its morphometry, Lake Aiguebelette has a very restricted littoral area. Hence, the lake cladoceran community is essentially composed of the planktonic species *Daphnia longispina* complex, *Eubosmina coregoni* (Baird 1857), *Eubosmina longispina* (Leydig 1860), *Bosmina longirostris* (O.F. Müller 1776) and *Diaphanosoma brachyurum* (Liévin 1848) (Balvay & Druart, 2008). *Acantholeberis curvirostris* (O.F. Müller 1776), *Alona affinis* (Leydig 1860) and *Chydorus* sp. were found in the rare littoral areas (Balvay & Druart, 2008).

II.3.2. Zooplankton sampling

Living zooplankton was collected monthly between January 2009 and February 2010, by one vertical haul from a depth of 50m to the surface using a 200- μ m mesh conical net, at the lake deepest point. Zooplankton samples were preserved in 5% formaldehyde and counted from a subsample of known volume on an Olympus BX40 light microscope at a 100–200X magnification using the determination key of Flössner (1972) and Balcer et al. (1984). A minimum of 250 individuals has been counted by subsample. Because species and hybrids from the *Daphnia longispina* complex can hardly be discriminated, *Daphnia* were identified at the generic level. Similarly, although both *Eubosmina coregoni* and *Eubosmina longispina* are present in the lake, differentiation between both species from whole individuals is relatively ambiguous (Flössner, 1972). *Eubosmina* was hence identified at the generic level. Other taxa were identified at the species level (*Bosmina longirostris*, *Diaphanosoma brachyurum*).

In order to establish allometric relationships that could be used to estimate, from the size of the remains recovered in the traps, the size distribution of the source population, *Daphnia* postabdominal claws, *Bosmina/Eubosmina* antennules and total body length were measured on living individuals for each taxon at each sampling date. *Daphnia* and *Bosmina/Eubosmina* total body length was measured from the compound eye to the base of tail spine or mucro respectively. For all three taxa, significant allometric relationships could be established. Using an analysis of covariance (ANCOVA), these allometric relationships were shown not to depend on sampling dates for *Daphnia* sp. (Month: $F = 2.227$, $df = 2$, $P = 0.111$; Month * Postabdominal claw size: $F = 1.035$, $df = 2$, $P = 0.358$) and *Eubosmina* spp. (Month: $F = 1.095$, $df = 8$, $P = 0.367$; Month * Antennule size: $F = 1.449$, $df = 8$, $P = 0.176$). For *B. longirostris* not enough size measurements were available to resolve separate equations. Data of each month were pooled within a general equation of the allometric relationship (*Daphnia* sp.: body size = $10.0 * \text{postabdominal claw size} - 8.3$, $n = 155$, $R^2 = 0.951$, $P < 2.2 \times 10^{-16}$; *Eubosmina* spp.: body size = $1.3 * \text{antennule size} + 29.3$, $n = 284$, $R^2 = 0.767$, $P < 2.2 \times 10^{-16}$; *B. longirostris*: body size = $1.3 * \text{antennule size} + 123.6$, $n = 50$, $R^2 = 0.847$, $P < 2.2 \times 10^{-16}$).

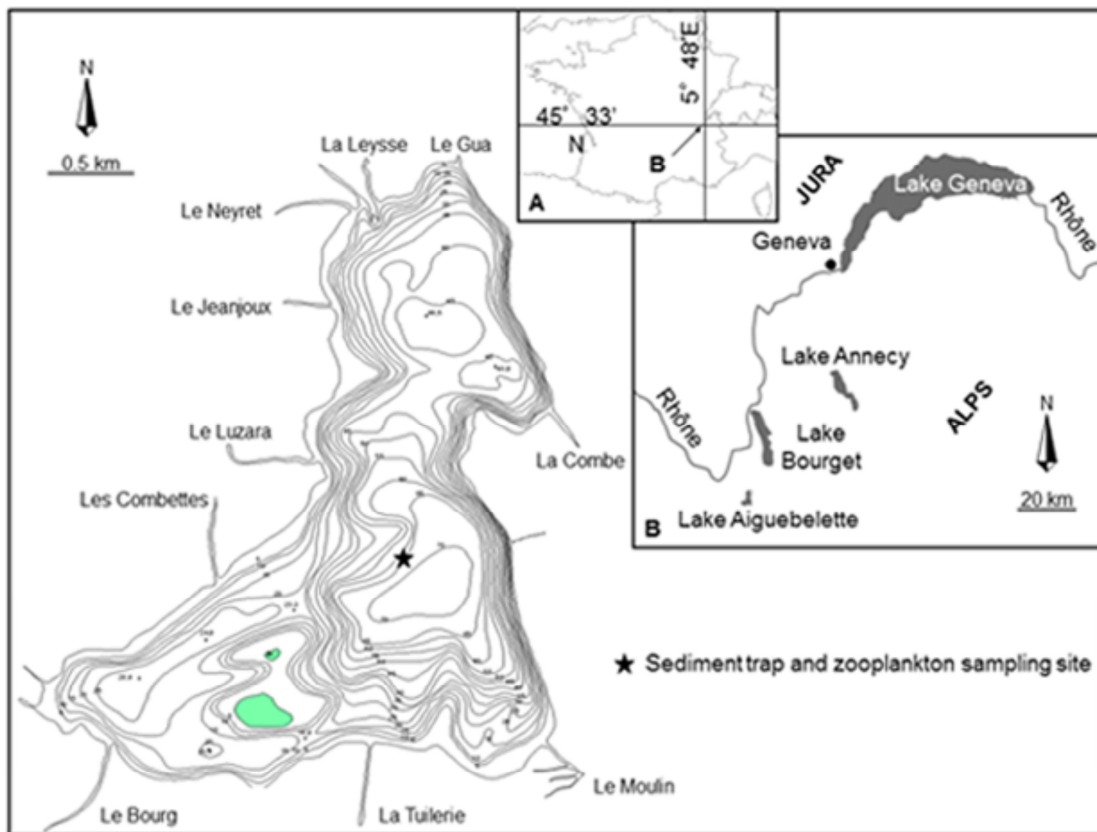


Figure II.1. Location of Lake Aiguebelette and bathymetric map showing the sediment trap and zooplankton sampling sites. Green forms correspond to islands.

II.3.3. Sediment traps

Two ST were suspended at the deepest point of the lake (Figure II.1), at two different water depths. The first trap was placed at a 15 m depth (just below the summer thermocline depth), and the other at 60 m deep (5 m above the lake bottom). Both ST consisted of six individual collecting cylinders in polyvinyl chloride grey. The internal diameter was 9 cm and the height was 80 cm to give a 9:1 aspect ratio, according to recommendations given by Bloesch and Burns (1980) and Gardner (1980). The traps were collected monthly between January 2009 and February 2010, as for living zooplankton sampling, and trap samples were preserved in C and N free Lugol in 50 ml vials before treatment.

Cladoceran remains of different trap samples were analysed according to Frey (1986). Trap samples were boiled in 100 ml of 10% KOH for 30 min to remove organic matter and then treated with 20 ml of 10% HCl to eliminate exogenous carbonates. Samples were passed through a 31- μ m mesh filtercup since prior tests showed that sieving on a 63- μ m mesh size resulted in a significant loss of remains, essentially *Daphnia* and *Diaphanosoma* post abdominal claws, consistently with previous observations from Nykänen et al. (2009).

Microscope slides were prepared with 0.1 ml of each sample and analysed using an Olympus BX41 light microscope, at a 100–200X magnification. A minimum of 400 cladoceran remains was counted from a subsample of known volume. The most numerous remains of each taxon were used to calculate the total abundance of individuals according to Frey (1986)'s equation. Cladoceran remains were identified using the determination keys of Szeroczynska and Sarmaja-Korjonen (2007). Most abundant and identifiable *Daphnia* and *Diaphanosoma* remains were postabdominal claws. Very few chydorid remains, mostly postabdomen, were counted in cladoceran trap samples. For *Bosmina*, most abundant and identifiable subfossil remains were headshields, allowing identification at the species level depending on the location of the lateral headpore (Szeroczynska & Sarmaja-Korjonen, 2007). Cladoceran trap samples were counted and identified with the same precision level as for water column samples (*Daphnia* sp. and *Eubosmina* spp., *Bosmina longirostris*, *Diaphanosoma brachyurum*).

The length of antennules and postabdominal claws was measured for *B. longirostris*, *Eubosmina* spp. and *Daphnia* sp. respectively, on a hundred remains for each taxon at each sampling date.

The monthly deposition of remains was expressed as a net accumulation rate (remains $\text{m}^{-2} \text{month}^{-1}$) and concentration per unit weight of dry sediment [remains (g dW) $^{-1}$]. To convert the volume-based concentration of remains to weight units, two of six individual collecting cylinders of each ST were pooled and analysed for sediment dry weight. Net accumulation rate of remains was calculated as the product of fossil concentration [remains (g dW) $^{-1}$] and sediment accumulation rate (g $\text{m}^{-2} \text{month}^{-1}$) in individual collecting cylinder of traps. Preliminary tests showed no significant differences on the percent contribution of each taxon between three individual collectors for a single date and a single depth, 60 m (Pearson's Chi-square test, February: $\chi^2 = 3.234$, $df = 8$, $P = 0.919$; April: $\chi^2 = 1.412$, $df = 8$, $P = 0.994$; May: $\chi^2 = 2.992$, $df = 8$, $P = 0.935$; June: $\chi^2 = 3.773$, $df = 8$, $P = 0.957$). Hence, monthly deposition of remains was estimated from a single individual collecting cylinder of ST for each taxon and each date at 15m and 60m-depth.

II.3.4. Data analyses

Non-parametric statistical tests were preferred to avoid problems related to the heteroscedasticity and the absence of normality. Composition of taxa (percentages) and seasonal dynamics (absolute abundances) such as size structure of cladocerans were compared between water column and trap samples using Spearman's rank correlation test. As both types of samples were not related to the same time-scales (water column samples are snapshots while trap samples integrate the sediment flux over one month), comparisons were performed between the ST sample at time t and the average water column sample between t and $t - 1$. When Spearman's rank correlation test showed significant correlations between the composition of taxa as well as size structure of cladocerans in trap and water column samples, Wilcoxon's signed rank test was used to address potential recurrent under- or over-representation of a given taxa / under- or over-estimation of size in the trap compared to water column samples.

The impact of taphonomic processes on the composition at the annual time scale was addressed comparing the annual percent composition between the water column and 60 m-trap samples using Pearson's Chi-square test.

All statistical analyses were performed on R2.11.0 statistical software (<http://www.r-project.org/>).

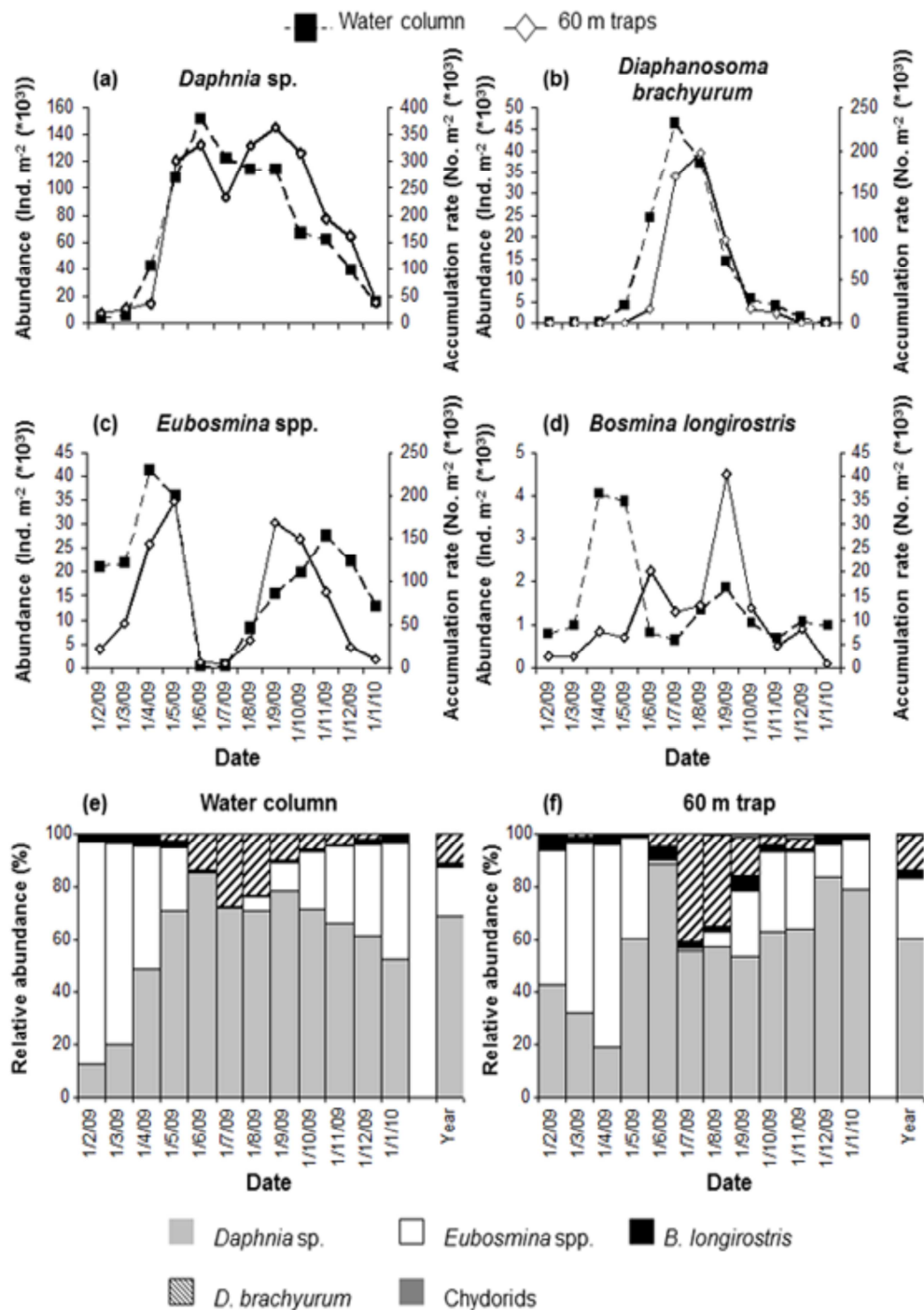


Figure II.2. Seasonal changes of the abundance of living cladoceran communities in the water column (*closed squares*) and accumulation rate of corresponding remains in 60 m-traps (*open diamonds*) for (a) *Daphnia* sp., (b) *D. brachyurum*, (c) *Eubosmina* spp. and (d) *B. longirostris* from February 2009 to January 2010. Relative abundance of different cladoceran taxa (e) in the total living population in the lake and (f) in the remain assemblages in the 60 m-traps.

II.4. Results

II.4.1. Comparison of the composition of taxa and dynamics of the cladoceran community between the water column and trap samples

On an annual basis, *Daphnia* sp. dominated the cladoceran community in the water column, representing on average 69% of the total abundance (Figure II.2). The contribution of *Eubosmina* spp., *D. brachyurum* and *B. longirostris* were 18, 11 and 2 % respectively (Figure II.2). All cladoceran taxa exhibited marked seasonal dynamics over the study year (Figure II.2a–d). *Daphnia* sp. and *D. brachyurum* showed a unimodal seasonal dynamics peaking in late spring and early summer, during the lake stratification (Figure II.2a,b). *Daphnia* sp. dominated the cladoceran community in the water column from May 2009 to January 2010, with however a predominance shared with *D. brachyurum* from June to August (Figure II.2e). In contrast, seasonal dynamics of *Eubosmina* spp. was bimodal with peaks of abundance in early spring and fall (Figure II.2c). *Bosmina longirostris* exhibited its maximum abundance in early spring (Figure II.2d). Therefore, *Bosmina* sp. (*Eubosmina* spp. + *B. longirostris*) dominated the cladoceran community in the water column during the water mixing period and early stratification (Figure II.2e).

Over the whole study period, the accumulation rates of *Daphnia* sp., *Eubosmina* spp., *B. longirostris* and *D. brachyurum* remains were similar between the 15 and 60 m traps (Wilcoxon's signed rank test, *Daphnia* sp.: $P = 0.266$; *Eubosmina* spp.: $P = 0.077$; *B. longirostris*: $P = 0.129$; *D. brachyurum*: $P = 0.742$; Table II.2), hence allowing to restrict the analysis to the comparison between the water column and the 60 m trap samples. Remains from littoral species, such as chydorids, were found only sporadically in ST (but not in water column samples) and at very low abundance (<0.5% of total cladoceran remains) from August to November 2009 (Figure II.2f). Seasonal changes in deposition rates (whatever the considered abundance unit) in the traps closely mirrored seasonal changes in *Daphnia* sp., *D. brachyurum* and *Eubosmina* spp. abundances in the water column (Table II.2; Figure II.2a–c) while correlations were not significant for the least abundant taxa, *B. longirostris* (Table II.2; Figure II.2d).

Likewise, seasonal changes in the percent composition of *Eubosmina* spp. and *D. brachyurum* remains in the 60 m-trap samples were correlated to the source community ones (Spearman's rank correlation, *Eubosmina* spp.: $\rho = 0.776$, $P = 0.005$; *D. brachyurum*: $\rho = 0.821$, $P = 0.001$). Statistical tests failed in detecting significant seasonal correlation for the percent composition of *Daphnia* sp., but general trends were similar between trap and water samples with the highest proportions of *Daphnia* sp. found in the 60 m-trap samples as in the water column during the same period, from May 2009 to January 2010 (Figure II.2e,f). Month-by-month comparisons between trap and water column samples did not detect any recurrent under- or over-representation of *Eubosmina* spp. or *Daphnia* sp. but an over-representation of *D. brachyurum* proportion from July to September in the sediment trap (Wilcoxon's signed rank test, *Daphnia* sp.: $P = 0.909$; *Eubosmina* spp.: $P = 0.969$; *D. brachyurum*: $P = 0.031$). Over the whole survey, the respective annual contribution of *Daphnia* sp., *Eubosmina* spp., *B. longirostris* and *D. brachyurum* to the trap remains were quite similar to those observed in the source communities (Pearson's Chi-square test: $\chi^2 = 1.918$, $df = 2$, $P = 0.59$). Unlike dominant taxa, changes in the deposit of *B. longirostris* remains in 60 m-traps do not reflect seasonal changes of the abundance of *B. longirostris* in the source population (Table II.2; Figure II.2d). The correlation did not improve even when considering a 1- to a 5-month delay (results not shown).

Table II.2. Results of Spearman rank correlation test for (i) the comparison of temporal changes between living cladoceran communities and their corresponding remains in 60 m-traps and (ii) the comparison of temporal changes in the deposits of remains between 15 m- and 60 m-traps.

Categories	Variable	60 m trap	
		g dW ⁻¹	m ⁻² month ⁻¹
Water column (ind. m ⁻²)	<i>Daphnia</i> sp. (n = 12)	0.678*	0.902**
	<i>Eubosmina</i> spp. (n = 12)	0.706*	0.636*
	<i>B. longirostris</i> (n = 12)	0.343	0.252
	<i>D. brachyurum</i> (n = 12)	0.735**	0.771**
15m-trap (g dW ⁻¹)	<i>Daphnia</i> sp. (n = 12)	0.902**	
	<i>Eubosmina</i> spp. (n = 12)	0.937**	
	<i>B. longirostris</i> (n = 12)	0.783**	
	<i>D. brachyurum</i> (n = 12)	0.957**	
15m-trap (m ⁻² month ⁻¹)	<i>Daphnia</i> sp. (n = 12)		0.846**
	<i>Eubosmina</i> spp. (n = 12)		0.958**
	<i>B. longirostris</i> (n = 12)		0.867**
	<i>D. brachyurum</i> (n = 12)		0.957**

Cladoceran abundances were expressed as monthly total per unit area (Ind.m⁻²). Trap cladoceran remains were expressed as a concentration per unit weight of dry sediment (g dW⁻¹) and as the monthly net accumulation per unit area (m⁻² month⁻¹). Correlation analyses were done for a 1-year period (12 months) for each taxa. * and ** indicate that the P-values associated to the test were < 0.05 and <0.01 respectively.

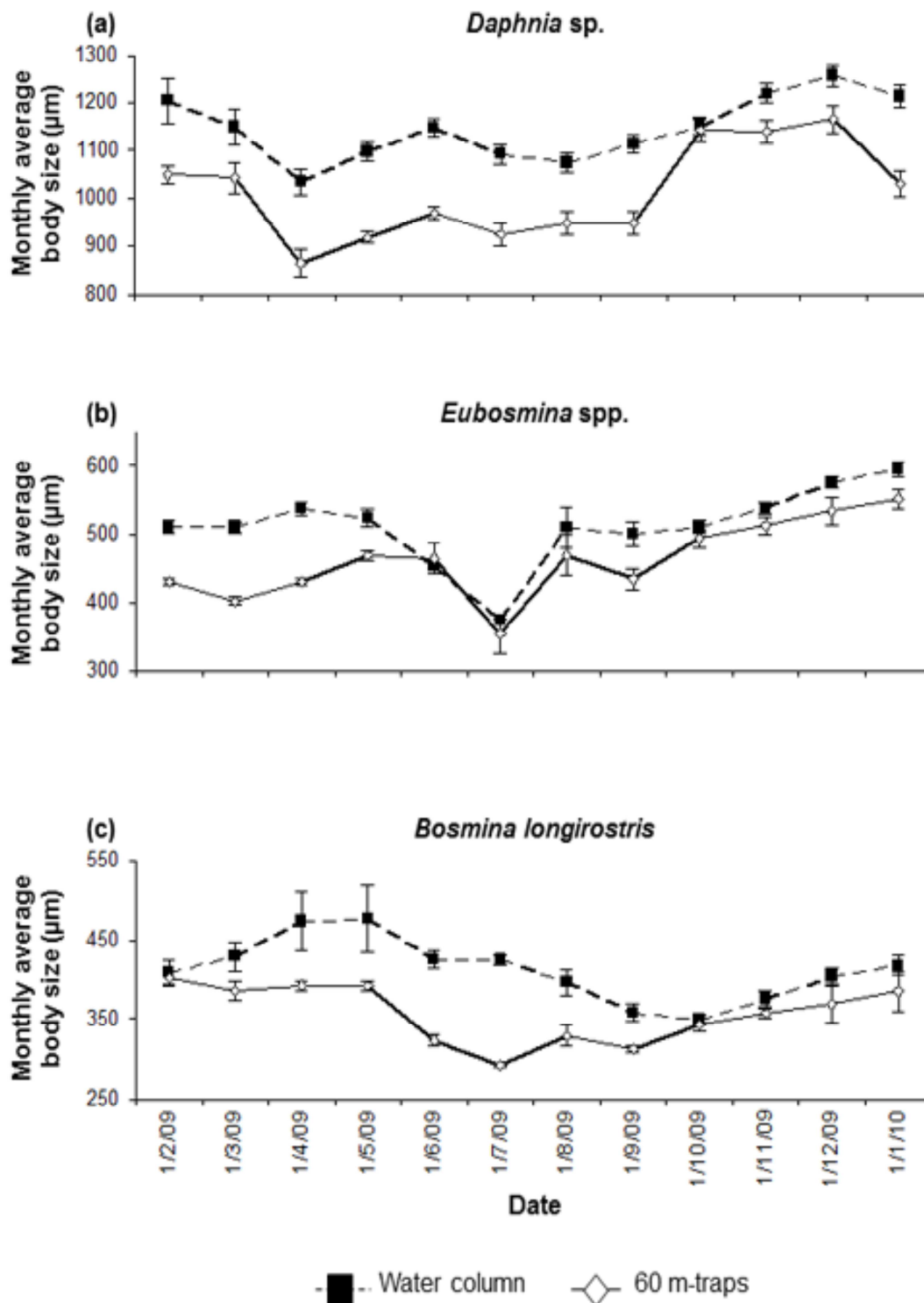


Figure II.3. Seasonal changes in the monthly average body size of individuals in the water column (*closed squares*) and in the estimated average body size of individuals in 60 m traps (*open diamonds*) for (a) *Daphnia* sp., (b) *Eubosmina* spp. and (c) *B. longirostris*. The latter were obtained by estimating of the average body size of the parent population from the sizes of remains (antennules and postabdominal claws) recovered in 60 m-traps according to the previously established allometric relationships (see "Material and methods" section). Bars represent the standard error of the measures.

II.4.2. Changes in the size structure of the cladoceran community in the water column and sediment traps

The average body size of *Daphnia* sp. and *Eubosmina* spp. individuals in the water column samples changed seasonally over the study year. For *Daphnia* sp., individuals were larger in December 2009 (average size (\pm S.D.): 1.257 (\pm 0.303) mm) and smaller in April 2009 (average size (\pm S.D.): 1.034 (\pm 0.277) mm). For *Eubosmina* spp., individuals were larger in January 2010 (average size (\pm S.D.): 0.596 (\pm 0.093) mm) and smaller in July 2009 (average size (\pm S.D.): 0.374 (\pm 0.137) mm). The estimated average body size of *Daphnia* sp., *Eubosmina* spp. and *B. longirostris* which produced the remains retained in 60 m-traps was every month significantly smaller, from 9 to 14 % on average, than the individuals size in the water column (Wilcoxon's signed rank test, *Daphnia* sp.: $P = 2.44 * 10^{-4}$; *Eubosmina* spp.: $P = 4.88 * 10^{-4}$; *B. longirostris*: $P = 2.44 * 10^{-4}$). The seasonal dynamics of average body size in the water column was however accurately reflected in 60 m-traps for *Daphnia* sp. and *Eubosmina* spp. (Spearman's rank correlation, *Daphnia* sp.: $\rho = 0.902$, $P < 2.2 * 10^{-16}$; *Eubosmina* spp.: $\rho = 0.650$, $P = 0.026$; Figure II.3a,b), while correlations were not significant for *B. longirostris* (Spearman's rank correlation: $\rho = 0.426$, $P = 0.169$; Figure II.3c). The comparison of the first and third quartiles of the size distribution between the source and the trap samples for each taxon explained this under-estimation of sizes in traps. This under-estimation of sizes arose from the under-representation of the individuals with the greatest size and subsequent over-representation of the smallest individuals in the 60 m-trap samples (Wilcoxon's signed rank test, first quartile: *Daphnia* sp.: $P = 0.008$; *Eubosmina* spp.: $P = 0.0009$; *B. longirostris*: $P = 0.001$, third quartile: *Daphnia* sp.: $P = 9.76 * 10^{-4}$; *Eubosmina* spp.: $P = 2.44 * 10^{-4}$; *B. longirostris*: $P = 0.014$). Closer comparisons between the size distributions of individuals in the water column and in trap remains were performed for each month and each taxon but showed no clear relationships (results not shown).

II.5. Discussion

By comparing cladoceran source community to their remains collected by deep-ST, this study aimed at addressing to what extent exuvia production, taphonomy and sedimentation occurring in the water column might contribute to alter the record of cladoceran historical changes in the sediment of a large deep lake.

II.5.1. Are biases in compositional fidelity similar to those documented in small and flat lakes?

Overall, our results showed that the cladoceran remains collected in ST provided a consistent picture of the composition of their source community for the dominant taxa *Daphnia* sp., *Eubosmina* spp. and *D. brachyurum*.

We did not observe any significant under-representation of *Daphnia* sp. and subsequent over-representation of *Eubosmina* spp., *B. longirostris* or *D. brachyurum* in traps compared to the water column at an annual time scale. A direct comparison of these results with previous studies is hampered by the heterogeneity of the approaches used in previous studies on the topic (Table II.1). Nevertheless, from Kattel et al.'s (2007) results, we determined *Daphnia* and *Bosmina* proportions in their ST, according to their sedimentary flux, this allowing a comparison of their representation between water column/ST. In Kattel et al.'s (2007) study performed in a small polymictic lake, *Daphnia* contribution was about half in traps samples compared to that in the water column, and the percent contribution of *E. longispina* and *E. coregoni* was consequently twice higher. The under-representation of *Daphnia* remains compared to their contribution in the water column has also been observed in studies comparing the composition of taxa of the source communities to that of the remain assemblages on SS or SC (Frey, 1960; Kattel et al., 2007; Nykänen et al., 2009) and such patterns have been commonly attributed to a higher degradation of *Daphnia* remains compared to *Bosmina*. Although this study focused on the taphonomic processes in the water column that may impact the fossil assemblages, an attention has been made to the sediment–water interface to estimate the representation of cladoceran (*Daphnia* sp., *Eubosmina* spp., *B. longirostris* and *D. brachyurum*) in sediments of Lake Aiguebelette. This representation was estimated through a loss rate (%) of cladoceran remains during their transportation from the water column to sediment surface.

The annual cladoceran remains fluxes to the SS were estimated, using a core-top samples (0–0.5 cm corresponding to years 2006–2007) from a short core collected in January 2008 from the deepest point of Lake Aiguebelette (unpublished results). Annual cladoceran remains fluxes to the SS and in ST were taken as the basis for estimating the loss rate (Kattel et al., 2007). Such data allowed us to assess loss rates for cladoceran remains in Lake Aiguebelette ranging between 72 and 99%, for both *Daphnia* sp. and *Bosmina* sp., whatever the considered abundance unit [remains (g dW)⁻¹ or remains m⁻² year⁻¹]. The rates are of similar order of magnitude as previous estimates on a small lake {86% [remains m⁻² year⁻¹] and 95% [remains (g dW)⁻¹] for *Daphnia* maximal loss rate, Kattel et al. (2007) and Kattel (2009) respectively}. Therefore, the magnitude of taphonomic processes might be similar between small and large deep lakes, and the physical characteristics of lake (i.e. morphometry and water depth) and mixing regime (i.e. thermal stratification) might not be directly responsible for the inconsistency between our results and those from most previous studies. Such patterns might rather arise either from specificities of the lake cladoceran community, or from some methodological issues.

First, the differences of representativity between *Daphnia* and *Bosmina* were usually observed in lakes in which *Daphnia* appeared in low abundance (Kattel et al., 2007; Kattel, 2009; Nykänen et al., 2009 in Table II.1), contrary to Lake Aiguebelette. It is acknowledged that species which appear in low abundance in the source community may be absent or show a low representation in the fossil assemblages compared to the most abundant species (Frey, 1986; Kattel et al., 2007; Nykänen et al., 2009) and this might contribute to under-representation of *Daphnia* in the fossil assemblages of these lakes. Another argument involving the degradation processes at the sediment-water interface might be brought up. Comparing the cladoceran composition between the source communities and the ST, this study focused on the taphonomic processes in the water column. Processes responsible of preferential degradation of *Daphnia* remains, as compared to *Bosmina* sp., might take place during burial, at the sediment–water interface. The percent contributions of *Daphnia* sp. and *Bosmina* sp. in the core-top sample from the above-mentioned short core were 69% and 31% respectively (unpublished results), i.e. quite similar to the average percent contribution of these two taxa in the water column and ST observed in this study. The absence of any differential degradation on cladoceran remains in Lake Aiguebelette might result from rather quick and direct sedimentation processes in an environment relatively undisturbed by sediment resuspension and transportation (Kerfoot, 1995).

The sieve-size used might also affect the counting of the remains (Nykänen et al., 2009). The most commonly used mesh sizes in paleolimnological studies range from 37 to 55 μm (Frey, 1986; Table II.1). However, the size of the postabdominal claw is directly related to the size of the animal itself (Kitchell & Kitchell, 1980; this study), and the proportion of claws passing through the sieve may, therefore, vary with the size structure of *Daphnia* population, regardless of the composition of taxa of cladoceran source community. In our preliminary tests, we found that only a very low proportion of *Daphnia* sp. and *D. brachyurum* claws (6% and 0% respectively) was retained on a 63- μm mesh sieve compared to a 31- μm mesh sieve. This under-estimation of the number of remains when using a relatively large sieve-size is consistent with the results of Nykänen et al. (2009), suggesting that for Lake Aiguebelette, the choice of the mesh size may also be an additional reason for the consistent representation of *Daphnia* sp. and *D. brachyurum* in ST. The observation, using an 80 μm -mesh sieve, of a strong underrepresentation of *Daphnia* sp. in sedimentary assemblages of Madison Lakes, in which the pelagic cladoceran community is also dominated by *Daphnia* sp. (Frey, 1960; Table II.1), reinforces the hypothesis that the sieve-size matters when counting *Daphnia* sp. and *D. brachyurum* remains.

In contrast to *Daphnia* sp., *Eubosmina* spp. and *D. brachyurum*, trap samples failed to accurately capture the seasonal changes in the abundance and average size of *B. longirostris*. Mismatches between remain assemblages and source communities were previously observed for rare cladoceran species (Nykänen et al., 2009), such as *B. longirostris* that contributed <5% to the total cladoceran communities in Lake Aiguebelette. Counting of rare species usually suffer from low accuracy (Kurek et al., 2010) even for the counting efforts performed in this study (400 remains/samples). Spatial and temporal deficiencies in zooplankton monitoring could also introduce biases in zooplankton counting resulting in this lack of accuracy (Nykänen et al., 2009) since it was not adapted to species with a high vertical heterogeneity (Pinel-Alloul & Ghadouani, 2009). More specifically, vertical hauls do not efficiently sample the lowest hypolimnion above the sediment, although *B. longirostris* has been shown to use hypoxic hypolimnetic depths as refuge against fish predation and interspecific competition (Horppila, 1997). In addition, the moulting rate is closely related to the developmental duration of eggs and the interval between births, because the exuviae are shed in near synchrony with the birth (Kerfoot, 1995).

Therefore, assuming that moulting rate of each taxon was the same as the turnover time of eggs, estimated from the temperature-dependent formulas from Vijverberg (1980), a zooplankton monitoring with a monthly sampling interval may not necessarily detect all changes in abundances of different taxa, since it exceeds the egg turnover time of each taxa. Last, cladoceran can exhibit a patchy distribution in large lakes (Pinel-Alloul et al., 1999) which is not revealed by the one-station sampling used in Lake Aiguebelette.

II.5.2. Are there some seasonal changes in the dynamics of remains deposition and could this affect the completeness of recorded time series?

ST samples captured accurately the compositional characteristic of cladoceran source community for the three taxa *Daphnia* sp., *Eubosmina* spp. and *D. brachyurum* over the whole study period, since the deposits of *Daphnia* sp. and *Eubosmina* spp. and *D. brachyurum* remains in traps matched the seasonal changes of the abundance of populations in the water column. Such a strong correlation showed that the sedimentation and degradation processes were rather constant over the study period. These results are in line with previous work on *Bosmina* sp. showing a seasonal correlation between observed *Bosmina* sp. population in the water column and the accumulation rate of remains in ST in a deep monomictic lake as a result of a deep-water environment relatively undisturbed by sediment resuspension and transportation (Kerfoot, 1995; Table II.1). Håkanson and Jansson (1983) developed a model, which allows predicting areas of erosion, transportation and accumulation in lakes. These areas differ in their exposure to the wind-induced currents and therefore in the intensity of resuspension processes. Resuspension primarily exists in erosion and transportation areas as a constant or periodic event, respectively. Their model also shows that lakes with a concave shape, such as Lake Aiguebelette (Figure II.1), have a more important accumulation zone compared to the zone of erosion and transportation than lakes with a linear or convex shape, more characteristic for small and flat lakes (Table II.1). The morphometry of Lake Aiguebelette thus could somehow explain the accurate representation of source community by fossil assemblages (Håkanson & Jansson, 1983; Hilton, 1985; Bloesch, 1995) at seasonal and annual time scales.

More specifically, the seasonal representation of *Eubosmina* spp., which has a peak of abundance in the water column during the water column mixing, could be expected to be biased as a result of a disturbance in sedimentary processes by water column mixing. However, during the water mixing, the lake morphometric characteristics might minimize resuspension due to currents too weak to create the necessary shear stress to disrupt the bottom sediment. For *Daphnia* sp. and *D. brachyurum*, the peak of abundance in the water column was observed during the lake stratification. In temperate lakes, the fading with depth of water movement resulting in a sediment resuspension is enhanced by thermal stratification. The thermal stratification may be considered as an important inhibitor of sediment mixing (Larsen & MacDonald, 1993; Bloesch, 1995). Winds, which generated mixing of the epilimnion, are efficiently blocked by thermocline and relatively quiescent hypolimnion waters remain. The sporadic record and very low abundance of remains from littoral species (i.e. chydorids) in Lake Aiguebelette ST (absence of lateral transport) also support the idea of an insignificant role of wind disturbances on the sedimentation of cladoceran remains in this study lake.

II.5.3. Does the size structure of the remains reflect that of the parent community all year round?

Seasonal changes in cladoceran average size were reflected in the trap samples. However, the estimated average size of cladoceran from trap remains was smaller each month (9–14 % on average) than the average body size of the source community in the water column. In addition, the size distribution of population as estimated from the trap remains was substantially different from the one measured in the source community. Such an underestimation of the size of *Bosmina* source community from remains assemblages has already been observed in Frains Lake (Kerfoot, 1981) where it has been attributed to the lateral transport of remains of the littoral *Bosmina* population which was characterized by individuals of smaller body size. Such processes might not contribute significantly to the patterns observed in Lake Aiguebelette as discussed previously. It might rather result from a size-dependent sensitivity of remains to degradation (i.e. a taphonomic process) or from the age structure characteristics of the source population (i.e. related to the production of exuvia).

Preferential breakage of larger remains during the transportation in the water column, as a result of age-related variation in the shape and density of remains (i.e. stage of instars), was previously observed for freshwater gastropods (Pip 1988). Should this process also occur for cladoceran remains, it could subsequently result in an under-estimation of cladoceran sizes in ST. Secondly, the proportion and size of remains retained in traps depend on the age structure characteristics of the source population (Kerfoot, 1981). The intermoult duration differs according to the life cycle stages, with a regular increase of time sequence between moulting from juvenile to reproducing adults (Anderson & Jenkins, 1942; Porcella et al., 1969). For instance, in *Daphnia magna*, for a temperature of 25°C juveniles—first 4 instars—have daily moults during the first 4 days, then levelling off to a fixed 2-day intermoult period for adolescent and adult—from the fifth instar (Porcella et al., 1969). Since younger individuals moult more often than older ones, and produce therefore more exuvia, their remains are over-represented compared to larger ones in trap samples. Consistently with such an hypothesis, the largest differences between sizes in the water column and traps were also observed for the periods characterized by the highest plankton abundance and remain accumulation rates (from May to September 2009 for *Daphnia* sp., from March to May 2009 and September 2009 for *Eubosmina* spp., and from April to September 2009 for *B. longirostris*). Therefore, the under-estimation of cladoceran average body size from remains collected in the traps might at least partly result from cladoceran growth dynamics.

II.5.4. Implications for paleolimnological studies

Using cladoceran remains as proxy to study long-term changes in source communities assumes that remain assemblages archived in lake sediments record the characteristics of source communities. Our results showed that, in Lake Aiguebelette, cladoceran remains production, sedimentation and taphonomic processes within the water column do not alter the CF of remains at seasonal and annual time scales. Likewise, temporal changes in the average body size of the dominant taxa in the source community were captured by trap samples. Our study yet essentially focuses on taphonomic processes operating in the water column, while remains are sedimenting, while most of the degradation processes act at the sediment–water interface.

Comparing fluxes between ST and SS, we could however show that, although degradation was substantial at the sediment–water interface, it operated at similar rates for *Bosmina* and *Daphnia* sp. Due to the absence of substantial littoral drift and sediment resuspension in deep lakes, recordings of the compositional and size characteristics of source communities in remain assemblages were also continuous throughout the whole year. Therefore, remain assemblages in ST provided a reliable annual picture of the contribution of *Daphnia* sp., *Eubosmina* spp. and *D. brachyurum* to the cladoceran source community in the water column. Hence, seasonal changes in remains abundance or size observed in the traps arose from seasonal changes in the source communities rather than from changes in the impact of taphonomic processes. The structuring of fossil assemblages seems driven by the same forces shaping the living communities (Davidson et al., 2007). Integration, over the annual time scale, of seasonal patterns by fossil assemblages reinforce the idea of the usefulness of cladoceran remains to reconstruct the past dynamics of food webs in deep subalpine lakes (Perga et al., 2010). Moreover, since the community structure of pelagic cladoceran (i.e. *Daphnia* and *Bosmina*) reflects the dynamics of pelagic food webs (Brooks & Dodson, 1965; Carpenter et al., 1985), cladoceran remains may be used to infer the impact of climatic changes on the functioning of lakes, through temperature-related changes on predator–prey relationships (Blenckner, 2005). Our results also highlighted cautions that should be accounted for in paleolimnological interpretations. One of these precautions—already raised by Nykänen et al. (2009)—is related to the representation of rare taxa, such as *B. longirostris* in Lake Aiguebelette. The reasons for the non-representation of rare taxa have not been clearly identified yet and may be related to random factors associated with sampling either in ST or in the water column. However, although this lack of similarity disturbs the signal of *B. longirostris*, sedimentation processes take place throughout the whole year, which suggests that these taxa may be used in terms of presence/absence in paleolimnological reconstructions. This study also highlighted the potential need for methodological improvement in the extraction of cladoceran fossil remains from lake sediment. Indeed, our observations reinforce the hypothesis of Nykänen et al. (2009) that sieve mesh size would be a possible source of biases. The impact of sieve mesh size on the quality of information given by fossil assemblages is not an isolated case for cladocerans, since other biological indicators such as chironomids are subject to similar issues (Verschuren & Eggermont, 2007).

The mesh size most commonly used in paleolimnological studies ranges from 37 to 55 μm , but according to the sieve mesh size used, the picture of abundance and size structure of cladoceran assemblages may vary. For instance, such biases might affect the interpretation of the Planktivory Index of Leavitt et al. (1989) based on the ratio [$\% Daphnia = \text{total } Daphnia / (Daphnia + Bosmina)$]. Practical aspects may therefore dictate the selection of the sieve mesh size while safeguarding data quality. Nykänen et al. (2009) discussed the difficulty of using a 25- μm sieve for routine work on Lake Vesijärvi, since it retained a large amount of detritus obscuring the remains and considerably prolonging the analysis. For large and deep lakes that are less subjected to inputs of allochthonous detritus, such as Lake Aiguebelette or the nearby Lake Annecy (Perga et al., 2010), using a 31- μm sieve does not make the analysis time any longer compared to a 63- μm sieve. Fossil assemblages of cladocerans in deep lake sediment may therefore successfully document past changes in source communities as long as taphonomic biases are considered. These fossil assemblages do not represent a time-averaged image but rather a direct record, at monthly scale, of the changes in source community structure. Because cladocerans such as *Daphnia* sp. produce ephippia, the fossilized forms can also provide access to information on evolutionary changes in cladoceran communities in response to lake perturbation (Weider et al., 1997; Mergeay et al., 2004; Brede et al., 2009). Unlike cladoceran subfossil remains, *Daphnia* ephippia only capture a short-time window, which is relevant since it results from environmental disturbance. As a result, the representation at high temporal resolution of the cladoceran source community by subfossil remains and the presence of ephippia in the sediment might provide a framework for studying ‘eco-evolutionary dynamics’ (Fussmann et al., 2007; Palkovacs & Hendry, 2010).

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III. Trajectoire écologique des communautés et perturbations multiples

Local forcings affect the vulnerability and responses of lake food webs to climate warming.

Soumis dans Ecology

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III.1. 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 its ecological state and thus on local anthropogenic pressures. We tested this hypothesis performing 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 time, of the pelagic food web. Trajectories of the cladoceran communities were compared between the three study lakes (Lakes Geneva, Bourget and Annecy) over the last 70-130 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 shown to be not equally affected by climate warming between lakes. In Lake Annecy, which is the most nutrient-limited, the cladoceran community was shown to be essentially controlled by local stressors, with no significant effect of climate warming. In contrast, the more eutrophicated 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 local stressors, and especially past and current nutrient inputs, but also changes in fish predation pressure through fisheries management practices.

III.2. Introduction

While the past, present and future climate variability is relatively well described (IPCC 2001) and increasingly acknowledged as an important driver of lake ecosystems (George and Harris 1985, Adrian et al. 1995), our understanding of the mechanisms by which climate affects lakes is still quite 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 both 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 might vary depending on the nature and on the 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 imply to hierarchize and scale up these different pathways (Leavitt et al. 2009). Achieving such an objective yet requires long-term datasets that can be obtained using paleolimnological reconstructions spanning time ranges long enough to encompass pre- and post-disturbance periods (Battarbee 2000).

In that aim, lots of efforts have been dedicated to reconstruct 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 (i) there are highly climate sensitive (ACIA 2004) and (ii) their remoteness allows obtaining a signal of their response to climate change that is not obscured by noise from local human influences (Battarbee et al. 2002). However, although these studies have considerably improved our understanding of the ecological consequences of climate change on polar and alpine lakes, the geographical non-uniformity in climate changes (that depend on the latitude, longitude and altitude, Blenkner and Hillebrand 2002, Livingstone et al. 2005) may however limit the generalization of such observations to other climatic regions.

The impact of climate variability on temperate lakes has been quite less investigated and most of the knowledge was provided from the study of long-term data series, hence restricting the implications of these results to the few lakes that have been subjected to long-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., De Stasio et al. 1996, Straile et al. 2003, Winder and Schindler 2004). Their trajectories facing global changes may also be largely complexified by interactions between climate and local stressors, since 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 reconstructions 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 forcing (e.g., Hausman et al. 2002, Wissel et al. 2011).

The purpose of this work was to compare, over the last century, the responses of the pelagic food web of three temperate, large and deep subalpine lakes submitted to rather similar climate variability but varying intensities of analogous local forcings (changes in nutrient inputs and fisheries management practices). The overarching aim was to scale up the role of local pressures versus climate warming on the responses of the pelagic food web over the past century. Our working assumption was that the pelagic food web of these three lakes should show similar responses to climate warming, consistently with Straile & Adrian (2000)'s findings. The alternative hypothesis was that because these lakes have been under different anthropogenic local forcings, the response of their pelagic food web to climate warming should be distinct (Umbanhowar et al. 2011). For such purposes, long-term changes in 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 other paleo-proxies since they are highly sensitive and quickly react to all three considered local and global forcings (lake nutrient levels, fisheries management practices and climate). Indeed, zooplankton, and cladoceran 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 structure of cladoceran prey community by top-down effects (Brook and Dodson 1965, Gliwicz and Pijanowska 1989).

Last, climate warming may affect cladoceran community, directly through its influence on biological processes (Moore et al. 1996) and indirectly since species-specific differences in response 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, Jeppesen et al. 2010). Hence, we considered that temporal alterations in the composition and size structure of cladoceran community should mirror the impacts of the considered forcings on the pelagic food web.

III.3. Material and methods

III.3.1. Study sites

Lakes Geneva, Bourget and Annecy are all warm-monomictic 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 Lake Geneva, Bourget and Annecy respectively. These three lakes formed during the last glaciation of Würm, about 19 000 years ago, by the retreat of large glaciers of the Quaternary within the Molasse Basin (Kilian 1915). The geographical vicinity of these lakes, with Lakes Bourget and Annecy situated within 50 and 70 km, respectively of Lake Geneva, places them within a similar climatic context characterised mostly by a global increase in temperature (Auer et al. 2007). All three lakes are currently submitted to long-term monitoring surveys, started in 1957 for Lake Geneva (managed by the International Commission for the Protection of Lake Geneva Waters and the INRA, French National Institute for Agronomical Research), 1996 for Lake Annecy (managed by the Intercommunal Association of Lake Annecy and INRA) and 2004 for Lake Bourget (Lake Bourget water agency and INRA).

As many water bodies in industrialized countries, Lakes Geneva, Bourget and Annecy underwent a phase of eutrophication beginning in the mid-20th century. The magnitude of eutrophication, however, differed between lakes. In Lake Annecy, nutrient abatement measures were undertaken as soon as 1967 when maximum lake total phosphorous concentration ([TP]) was <20 µgP L⁻¹ (oligo-mesotrophic status, Perga et al. 2010).

Since then, lake [TP] has been constantly decreasing and is now $< 6 \mu\text{gP L}^{-1}$. Nutrient abatement strategies were lagged behind for the two other lakes and were undertaken in the late 1970's- early 80's, while lakes had already switched to a settled eutrophic status (max [TP] were 90 and 130 $\mu\text{gP L}^{-1}$ for Lake Geneva and Bourget respectively). In both lakes, [TP] has been successfully reduced over the last 30 years to levels more typical for oligo-mesotrophic lakes (23 and 17 $\mu\text{gP L}^{-1}$ for Lake Geneva and Bourget respectively in 2010; INRA long-term observatory database).

Fishing is a central economic activity on the three study lakes. They host similar fish communities, typical for peri-alpine lakes (whitefish, *Coregonus lavaretus*; arctic char, *Salvelinus alpinus*; trout, *Salmo trutta lacustris*; pike, *Esox lucius*; perch, *Perca fluviatilis*; burbot, *Lota lota* and roach, *Rutilus rutilus*; Gerdeaux et al. 2006). Whitefish, which is essentially zooplanktivorous in peri-alpine lakes (Berg et al. 1994), is one of the major fisheries resources in these lakes and fisheries management practices, centered on this particular species, are thus expected to trigger changes in cladoceran communities throughout top-down effect. Originally autochthonous in Lakes Geneva and Bourget, whitefish has been introduced in Lake Annecy in 1886 (Le Roux 1908). In Lake Geneva, however, the two indigenous subspecies were overfished and whitefish disappeared by the end of the 19th century. It was re-introduced later on (from 1923, Keith and Allardi 2001) using individuals from the nearby Lake Neuchâtel. Whitefish stocking is a common practice to support the fishery recruitment in these lakes (Gerdeaux et al. 2006). Whitefish was stocked in Lake Annecy sporadically from 1900 to the 1930s and then annually from 1936 to 1997 while, in Lake Geneva, it was annually stocked since 1970. In Lake Bourget, stocking was performed every year during 1943-1965 and 1986-2008 (Champigneulle et al. 2001).

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

III.3.2. Coring and chronology

Several short sediment cores (30 to 72 cm deep) were collected in lakes deepest points in May 2010 (Geneva) and February 2009 (Bourget) using a quadruple gravity corer (UWITEC, Mondsee, Austria).

Sediment dating was performed from one reference core for each lake using radiometric methods (measurement of ^{210}Pb , ^{226}Ra , ^{137}Cs and ^{241}Am activities) and varve counting (see Appendix A for details). The cores (LEM10_P8, for Lake Geneva and LDB09_P3, for Lake Bourget) on which paleolimnological analyses were performed were correlated to the reference core using lithological tie points. Annual laminated sediments and radionuclides provided accurate chronology for high-resolution sampling in Lakes Bourget and Lemman (see Appendix A for details). Cores were sampled annually according to the varve counting in their top laminated part. Bottom non-laminated sediments were dated as a function of average annual sedimentation rate estimated from ^{210}Pb analysis. Sampling and dating details of Lake Annecy were described in (Perga et al. 2010).

III.3.3. Subfossil cladocerans analysis

For cladoceran remains, details on extraction from sediment and analysis (countings and measures) can be found in Alric and Perga (2011). *Daphnia* (*D. longispina* 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 weight of dry sediment [remains (g dry wt) $^{-1}$] and net accumulation rate (remains cm $^{-2}$ year $^{-1}$) for each taxa (see Appendix A for details). The length of *Daphnia* 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* population (Perga et al. 2010, Alric and Perga 2011). The length of *Daphnia* 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, Brook and Dodson 1965).

III.3.4. Environmental forcing

Climate variability involves various components, among which changes in air temperature and precipitations (Leavitt et al. 2009). For each lake, dataset of annual and seasonal air temperature as well as precipitations have been extracted from the Histalp database (www.zamg.ac.at/histalp/), according to lakes geographical coordinates (Auer et al. 2007).

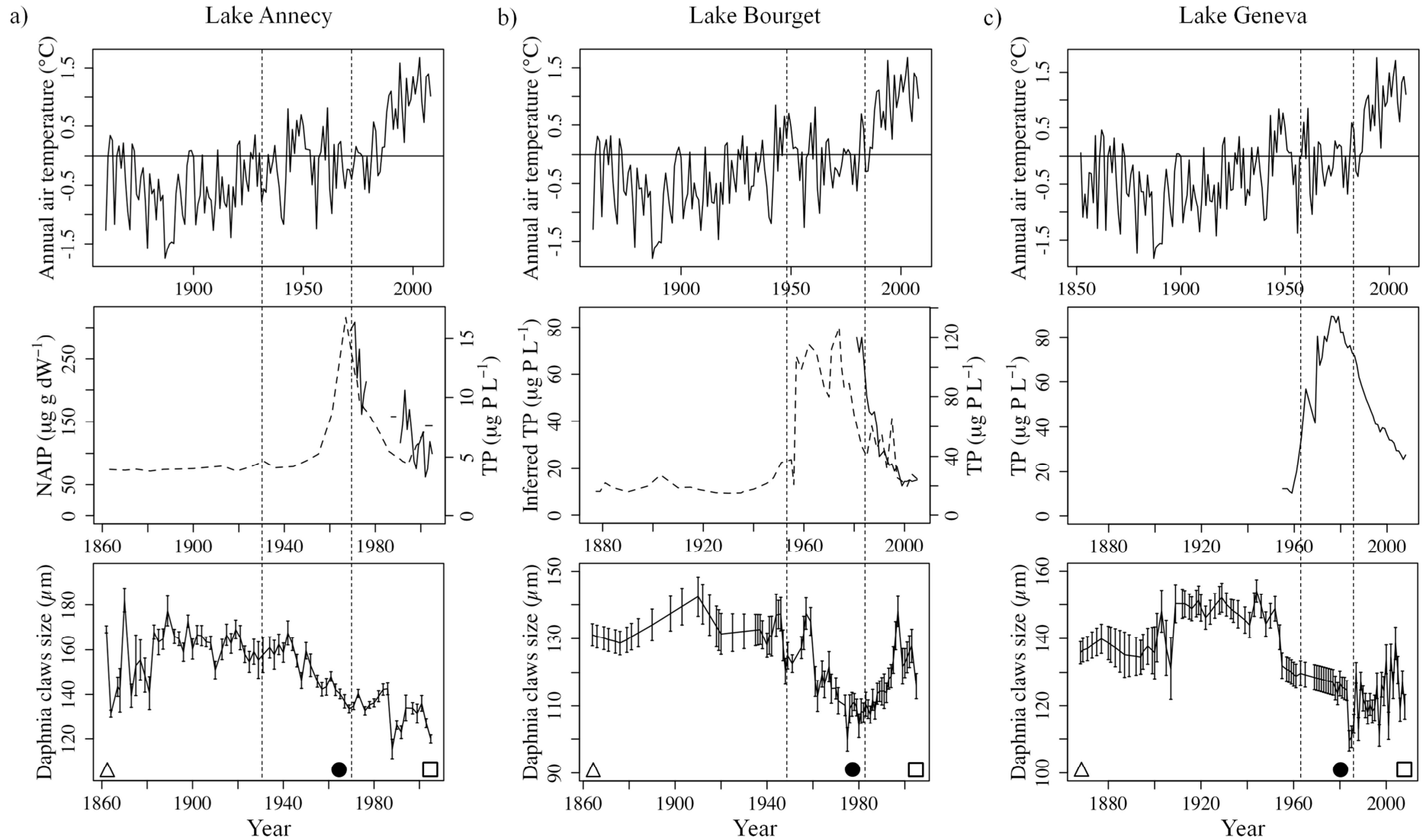
Temporal changes in lake water P concentration were assessed resorting to three different approaches. For Lake Geneva, annual measurements of winter P concentrations in the water column were available from 1957 to 2010 (see Anneville et al. 2002 for more details of the measurements of the phosphorous concentration in the water column). For lakes Annecy and Bourget, such direct, long-term measurements were not available and changes in P concentrations were reconstructed from sediment archives. For Lake Annecy, temporal changes in total P were reconstructed from changes in the concentrations in non-apatite inorganic phosphorous (NAIP) along the sediment core, since NAIP trend may be closely related to the total P (Williams and Jaquet 1978). NAIP provided also a good estimate of the bio-available fraction of phosphorous (Williams et al. 1980) and may be directly derived from anthropogenic activities (Williams and Jaquet 1978, Loizeau et al. 2001). For Lake Bourget, this technique did not provide satisfying results (see Giguet-Convex et al. 2010) and temporal changes in P concentration over the study time period were reconstructed using a diatom-transfer function. A diatom-based inference model for total phosphorous based on 86 surface sediment samples collected in lakes around the Alps along a trophic gradient (Wunsam and Schmidt 1995) was applied to a diatom biostratigraphy (Berthon et al., unpublished data) by the weighted averaging regression method using ERNIE software (Juggins 2001).

III.3.5. Statistical analyses

Chronological clustering analyses 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 of each sediment core (see Appendix A for details).

In order to investigate the relationships between the trajectory of cladoceran community (summarized from a principal components analysis (PCA) on remains abundance) and environmental forcing as well as to separate and quantify their influences, a generalized additive model (GAM, Hastie and Tibshirani 1990) was used (see Simpson and Anderson 2009 and Appendix A for details).

All statistical analyses were performed on R2.11.0 statistical software (<http://www.r-project.org/>).



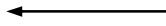


Figure III.1. Long-term changes in average annual air temperature (anomalies from the 1901-2000 average), phosphorous (P) concentrations (see “Material and methods” section for more details on the methods used to determine P concentration according to the lakes), and the length of *Daphnia* claws in (a) Lake Annecy, (b) Lake Bourget and (c) Lake Geneva. Symbols correspond respectively to the periods of (open triangles) pre-eutrophication, (closed circles) eutrophication and (open squares) re-oligotrophication. These time periods are characterized by changes in intensity of the different external forcings.

III.4. Results

III.4.1. External forcings

In all three lakes, annual and seasonal air temperatures exhibited a common and significant increasing trend from the last 1980s. Between 1986 and 2009, mean annual air temperature has increased by more than 1°C as compared with the prior period for all lakes. Increased annual air temperature essentially resulted from warmer winters (+ 1.6-1.7° C). No trends were observed for annual and seasonal precipitations in the three lakes (Mann Kendall’s tau test, $P>0.05$).

P concentrations, as reconstructed from paleolimnological proxies in Lakes Bourget and Annecy, exhibited a significant temporal evolution with a unimodal shape, which mirrored accurately changes in the lake total P concentrations based on monitoring and historical data (Figure III.1a,b). Before 1940s and 1930s, respectively for Lakes Bourget and Annecy, the weak P concentrations suggested low nutrient inputs to the lakes (pre-eutrophication period). Subsequently, P concentrations gradually increased (early eutrophication period), then dramatically (intense eutrophication period) peaking in the late 1970s for Lake Bourget and in the late 1960s for Lake Annecy, consistent with the maximum eutrophication period. From these maximum eutrophication periods, reconstructed P concentrations and monitoring data can be directly compared and showed a similar decreasing trend of P concentrations in both lakes as a result of decreased nutrient inputs to the lakes (re-oligotrophication period). For Lake Geneva, we did not have access to a reconstruction of P concentrations over such a time period but monitoring data spanned the whole period of eutrophication as well as the current period of re-oligotrophication (Figure III.1c).

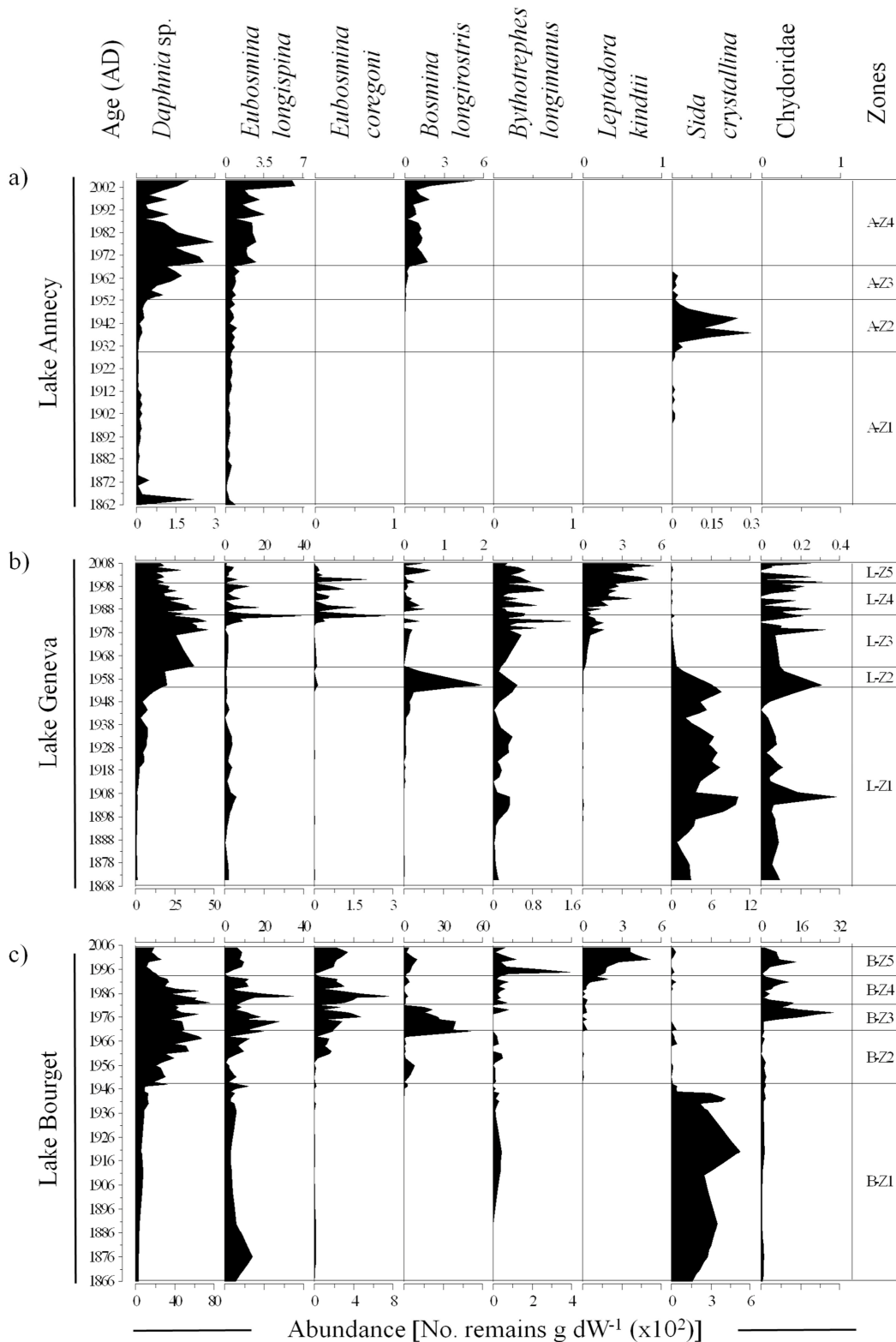


Figure III.2. Stratigraphic abundance of cladoceran remains in sediment cores (as absolute concentration per unit weight of dry sediment) of (a) Lake Annecy, (b) Lake Geneva and (c) Lake Bourget. Zones correspond to the time periods identified by chronological clustering on core 06-03 for Lake Annecy,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

Temporal changes in the average size of *Daphnia* post-abdominal claws indicated modifications in predation pressure over time. In pre-eutrophication period, the average size of *Daphnia* post-abdominal claws was large in all three lakes suggesting a relatively low predation pressure (Figure III.1a–c). In all three lakes, changes in *Daphnia* size, and hence predation pressure, were first triggered by eutrophication, with *Daphnia* sp. size decreasing, from the early eutrophication and all over the intense eutrophication period. *Daphnia* postabdominal claw got about 20% smaller as compared to the pre-eutrophication period in average, across all three lakes. *Daphnia* size responses (and hence fish predation pressure on *Daphnia*) to re-oligotrophication yet diverged between lakes: *Daphnia* sp. size kept on shrinking in Lake Annecy while TP was decreasing, while *Daphnia* size remained low but stable in Lake Geneva. In contrast, *Daphnia* size increased back in Lake Bourget during the re-oligotrophication period, attesting of a released fish predation pressure on *Daphnia*.

III.4.2. Trajectories of cladoceran community in lakes

Overall, 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 kindtii* (Focke 1844)] and two littoral taxa [Chydoridae and *Sida crystallina* (O.F. Müller 1776)]. The eight taxa were found in Lakes Geneva and Bourget while only four taxa (*Daphnia* sp., *B. longirostris*, *E. longispina* and *S. crystallina*) were found in Lake Annecy. Chronologically constrained cluster analyses identified five cladoceran assemblage zones for Lakes Geneva and Bourget and four zones for Lake Annecy (Figure III.2a–c). Cladoceran assemblages in zones 1, 2 and 3 (time periods of gradual increase in TP) for each lake showed similar changes in their structure in response to lake eutrophication while trajectories diverged from the zone 4 corresponding to the beginning of gradual decrease in TP.

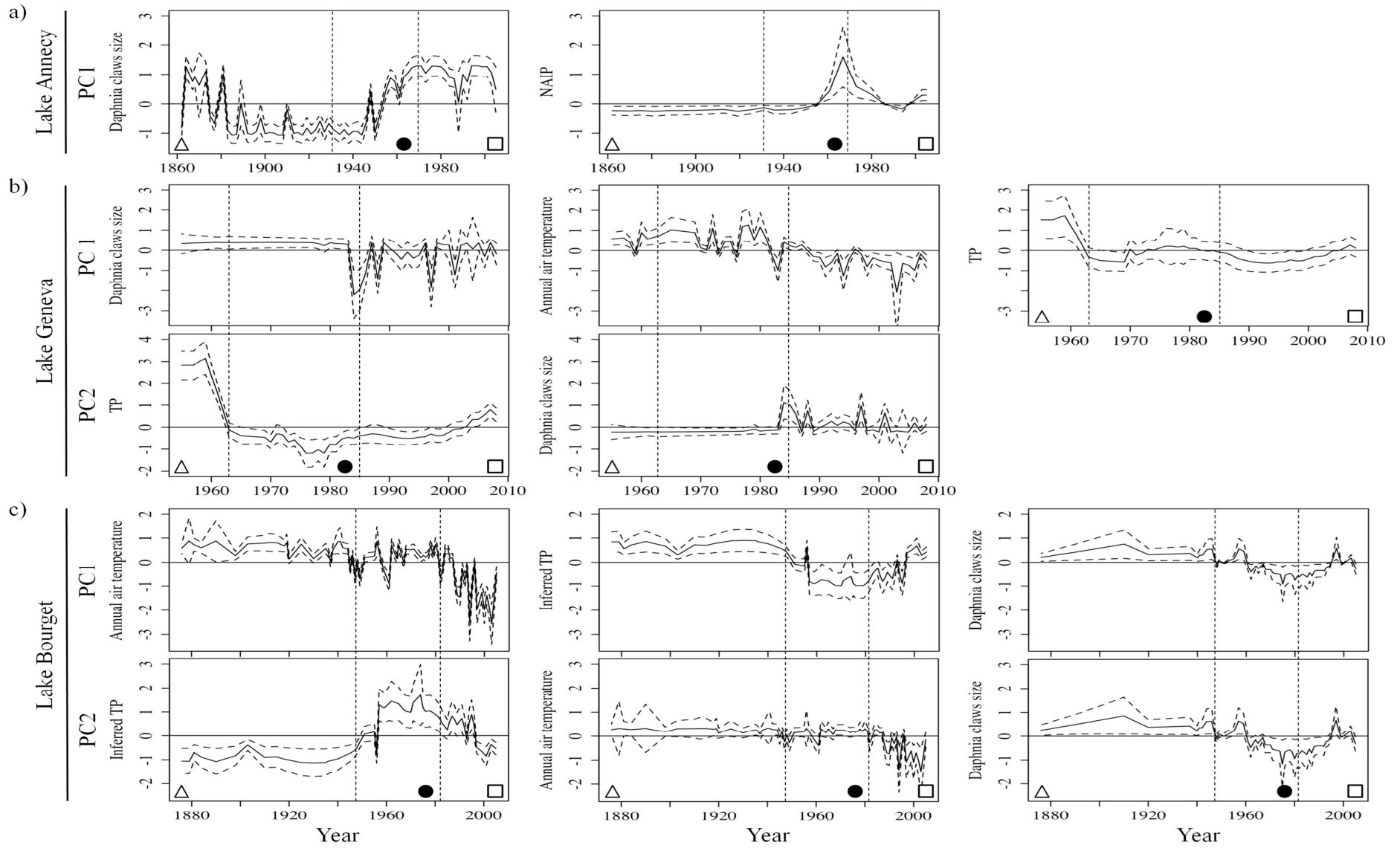
In zone 1 (before the 1940s for all lakes, corresponding to time periods of low TP), *Daphnia* sp., *E. longispina* and *S. crystallina* remains were found in low abundance but exhibited the greatest contribution to total assemblages. *Bosmina longirostris* and *E. coregoni* were found only in Lakes Geneva and Bourget, and in very low abundances.

Zones 2 (before the 1960s for Lakes Geneva and Bourget and the mid 1950s for Lake Annecy) and 3 (during the 1970s for Lakes Geneva and Bourget and the 1960s for Lake Annecy) corresponded to time periods of respectively slow and intense increase in TP for all lakes and were characterised by (i) a significant increase of *Daphnia* sp. abundance (from six- to twelve-fold) and (ii) changes in the composition of *Bosmina* remains, with the appearance (Lake Annecy) or the increased contribution of *B. longirostris* to assemblages [from less than 10% in 1946 up to 60% in 1955 for Lake Geneva and from less than 20% in 1947 up to 89 and 73% in 1957 and 1971 for Lake Bourget (Figure III.2a–c; Appendix B)]. *Bosmina* sp. (*E. longispina* in the three lakes plus *E. coregoni* in Lake Geneva and Bourget) abundances further increased during eutrophication period. During this period also, *S. crystallina* abundance decreased steadily in the three lakes and chydoridae abundances increased in Lakes Geneva and Bourget (Figure III.2b,c; Appendix B).

Zone 4 (from the 1980s for Lakes Geneva and Bourget and the 1970s for Lake Annecy) corresponded to time periods of reduce in TP for all lakes but coincided also to the beginning of significant changes in air temperature. In this stage, the response of cladoceran communities diverged between the three lakes. *Daphnia* sp. abundance started decreasing in both three lakes with yet different magnitudes (Figure III.2a–c; Appendix B). 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 Lake Geneva and Bourget) remained higher even in zone 5 than during the pre-eutrophication period from two- to ten-fold, 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 abundance of the predatory cladocerans *L. kindti* and *B. longimanus* was high in Lakes Geneva and Bourget in zone 5 while these species were not detected in Lake Annecy (Figure III.2a–c).

Table III.1. Relative contributions of the different cladoceran taxa to the two first principal components (PC1 and 2) for all three lakes.

Lake	Taxa	PC1	PC2
Geneva	<i>Daphnia</i> sp.		-0.488
	<i>B. longirostris</i>		0.527
	<i>E. coregoni</i>	-0.460	
	<i>E. longispina</i>	-0.478	
	<i>B. longimanus</i>	-0.215	
	<i>L. kindtii</i>	-0.317	
	<i>S. crystallina</i>		0.501
	Chydoridae	0.267	
Bourget	<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. kindtii</i>	-0.384	
	<i>S. crystallina</i>	0.528	
	Chydoridae		-0.452
Annecy	<i>Daphnia</i> sp.	0.571	
	<i>B. longirostris</i>	0.443	
	<i>E. longispina</i>	-0.640	
	<i>S. crystallina</i>		0.787



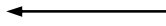


Figure III.3. Temporal contribution of covariates selected in final GAMs fitted to cladoceran PC1 and 2 for (a) Lake Annecy, (b) Lake Geneva and (c) Lake Bourget. The dashed lines are approximate 95% confidence interval on the contribution. Where the dashed lines include the zero lines, the contribution of the covariate is not statistically significantly different from the intercept. The order of covariates for each lake corresponds to the importance of their contribution to explain the fitted cladoceran PCs scores (see Appendix C for more details). Symbols correspond to the periods of changes in intensity of different external forcings (see Figure 1 for more details).

III.4.3. Additive models

In preamble to the additive models, PCA were performed for each lake over the taxa abundance datasets. The first two axes of PCA accounted for 62, 59 and 80% 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 show). The relative contributions of different taxa to the formation of the first and second principal components (PC1 and 2) are presented in Table III.1. Briefly, in Lakes Geneva and Bourget, PC1 accounted for the correlated changes in the contributions of *Bosmina* and predatory cladoceran species while PC2 essentially accounted for the negatively correlated changes in *Daphnia* contribution to total assemblages versus that of littoral species. For Lake Annecy, PC1 and PC2 represented changes in the composition of pelagic (*Daphnia* sp., *B. longirostris* and *E. longispina*) and littoral species (*S. crystallina*) respectively. Analyses of biostratigraphic sequences, PCA and even GAMs were similar whatever the considered unit for cladoceran remains (abundance in [remains (g dry wt)⁻¹] or fluxes [remains cm⁻² year⁻¹]).

The automatic selection procedure as well as the manual stepwise selection procedure of GAMs selected the same sets of covariates in the best-fitting models. The final GAMs were functions of different covariates among the lakes for both PC and explained between 37-80% of the deviance of PC1 and 2 scores (Appendix C). In Lake Annecy, covariates did not significantly model the PC2 scores. The fitted relationships between PC1 or 2 scores and the different covariates were mainly nonlinear in all lakes (edf > 1; see Appendix C). Only, PC1 scores displayed linear response to the changes in predation pressure and nutrient levels respectively for Lakes Bourget and Annecy (edf = 1; see Appendix C).

The scale up of the contribution of the fitted values of covariates to the GAMs differed amongst lakes and PCs. In Lake Annecy, average annual air temperature did not contribute significantly to fitted PC1 scores and the influence of predation pressure on PC scores was much larger than that of P concentration (Figure III.3a; Appendix C). In both Lakes Geneva and Bourget, all three covariates contributed significantly to fitted PC1 and 2 scores, although their respective importance changed between lakes and PCs (Figure III.3b,c; Appendix C). Fitted PC1 scores (related to *Bosmina* and predatory cladoceran dynamics) were essentially driven by average annual air temperature and P concentrations in Lake Bourget while they were driven by predation pressure and average annual air temperature in Lake Geneva (Figure III.3b,c; Appendix C). In both lakes, P concentration was the major contributor to fitted PC2 scores (accounting mostly for *Daphnia* versus littoral species dynamics) (Figure III.3b,c; Appendix C).

Although the relative magnitudes to which each covariate contributed to fitted PC scores differed between Lakes Geneva and Bourget, the temporal dynamics of the contribution of covariates were similar: P concentrations contributed for almost all over the study periods and the influence of fish predation pressure was more temporally limited. In addition, in both lakes, significant influence of air temperature occurred only 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 P concentrations suggesting a correlation between these two forcings while, in Lake Geneva, the contributions of predation pressure and air temperature were coupled from the late 1980s. In Lake Annecy on which we detected no significant climate contribution, the effect of predation pressure on changes of PC 1 scores was significant all over the study period with significant shifts in the 1880s and in the 1950s. P concentrations contributed significantly from the 1950s to the mid 1980s, i.e. periods of drastic changes in P concentrations.

III.5. Discussion

Our study intended to evaluate and scale up the effects of local forcings versus climate warming on the trajectory of cladoceran communities in three temperate, peri-alpine lakes submitted to similar climate warming.

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 favoured over the most commonly used diatom frustule remains.

III.5.1. Evaluating temporal changes in external forcings

Our approach required proxies for the three forcings considered herein. Direct access to long-term climate data through the Histalp dataset allowed the use of monitoring data rather than paleo-proxies for climate influence. Yet, as summarized by the Energy-Mass conceptual model (Leavitt et al. 2009), climate variability is much more than changes in precipitations (that were insignificant on our study period) and air temperature as we tested herein and also includes changes in atmospheric deposition, irradiance (PAR, UVR) and wind friction (see Leavitt et al. 2009 for more details). We therefore acknowledge that the role of climate variability on lake trajectories was only partly addressed within this study since we focussed essentially on the warming aspect of climate change. However, unlike shallow, boreal lakes (Wissel et al. 2011), alterations of the lake thermal regime because of increased air temperature are likely to be the main driver of climate-related changes in these large deep temperate lakes (e.g., Molinero et al. 2006, Obertegger et al. 2007). Thus the climatic components that were considered herein were likely to be amongst the most influential on the pelagic food web in these lakes.

Within paleolimnological approaches, past P concentrations have been quite usually inferred from diatom remains (Hall and Smol 1992). The P transfer-function established from the diatom data developed on 86 European lakes provided relevant results for Lake Bourget but was much less efficient for Lake Annecy. Actually, Lake Annecy trophic status shifted from ultra-oligotrophic to, at most, oligo-mesotrophic and is now back to ultra-oligotrophy.

However, lakes of very low trophic status are poorly represented in the dataset on which the transfer-function was calibrated and this consequently limited the ability of our transfer function to adequately reconstruct limited changes in P concentrations in oligotrophic lakes. Temporal changes in P water concentrations were hence inferred using other paleo-proxies (NAIP concentrations in the sediments). Although less commonly used and sometimes contested, the NAIP approach provided, in this peculiar case, results that were highly consistent with previous monitoring data and other paleo-proxies for nutrient inputs in lakes (i.e., sediment $\delta^{15}\text{N}$, Perga et al. 2010). Unfortunately, diatom biostratigraphy was not available for Lake Geneva and P concentrations were those measured during the long-term monitoring.

The third forcing factor included within this study was fisheries management practices. Unfortunately, neither long-term data for fish stocking in the three lakes nor Catch per Unit Efforts (CPUE) were available (and those that were for older time periods were not always reliable). In addition, temporal changes in total fish yields do not necessarily reflect those in fish stocks over such long time-periods since fisheries practices and regulations have been strongly modified over this time course. Temporal changes in fisheries practices were then approached through changes in fish predation pressure on zooplankton (and more specifically *Daphnia*). Indeed, CPUE and cladoceran community structure have been shown to be so related in lakes that cladoceran-CPUE transfer functions have been developed and applied in both shallow and deep lakes (Jeppesen et al. 1996, Manca et al. 2007). Amongst all zooplankton community characteristics, *Daphnia* body size was shown to be strongly dependent on fish predation (Kerfoot 1974). Hence, although *Daphnia* body size may also respond to other factors such as the quantity and quality of food resource and climate (Hart and Bychek 2011), predation is such a strong structuring factor that CPUE were found as strongly related to the size of *Daphnia* resting eggs, itself strongly correlated to total *Daphnia* body size (Jeppesen et al. 2002). Unfortunately, resting eggs were very rare in the sediments of our study lakes (Perga 2010), precluding the use of previously established transfer functions. The size of *Daphnia* post-abdominal claws appeared to be a more adequate proxy for fisheries practices, considering the large quantity found in sediment and its linear relationship with *Daphnia* body length (Kitchell and Kitchell 1980, Alric and Perga 2011). Size structure of *Daphnia* population could then be perceived as a smoothed picture of fish planktivory.

Strong changes in the intensity of fish planktivory can be induced by fisheries management practices, and especially selective removal of predatory fish by angling or stocking of zooplanktivorous fish, but so could changes in lake productivity (Jeppesen et al. 2007) or climate-driven changes in fish recruitment (Jeppesen et al. 2007, Anneville et al. 2009). The use of GAM allowed though to distinguish changes in fish planktivory that were related to bottom-up or climate influences, from those that most likely resulted from fisheries management practices.

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.

III.5.2. 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 cladoceran were driven by different combinations of forcings.

Before the 1980s, P was the main driver of the pelagic food web. Increased TP from the 1940s triggered similar changes in the cladoceran community structure although maximum TP levels differed between lakes. Increased nutrient inputs sustained a higher primary production which in turn allowed the increase of pelagic cladoceran abundance (McCauley and Klaff 1981), in particular *Daphnia* sp., and resulted in a drastic decline in species more typical for shallow habitats (*S. cristalina*) due to lower water transparency and reduction of littoral habitats. Consistent patterns were observed in other deep subalpine lakes (Ravera and Parise 1978, Manca et al. 2007). In all lakes, decrease in *Daphnia* body size coincided with the beginning of eutrophication, attesting that the intensity of top-down control by planktivorous fish increased with higher nutrient concentrations. In Lake Annecy, whitefish was considered as the main fish species responsible for such increase in size-selective predation during this period in Lake Annecy (i.e., oligomesotrophic at its maximum eutrophication, Perga et al. 2010) since whitefish stocks reach maximum values in oligomesotrophic lakes (Jeppesen et al. 2000, Gerdeaux et al. 2006).

In the two other lakes which were more intensively eutrophicated, it is very likely that this strong predation pressure on zooplankton was maintained by a compensatory shift in the contribution to the predation pressure from whitefish to juvenile perch and roach, since perch as well as roach were shown to dominate the fish community in of these lakes for nutrient status higher than mesotrophic (Jeppesen et al. 2000, Gerdeaux et al. 2006). Another striking pattern 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 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. By reducing *Daphnia* size, whitefish selective predation could indirectly reduce their competitive interaction with *Bosmina* sp. and allow the establishment of the new *Bosmina* species. This interpretation is consistent with indirect facilitation processes previously tested in mesocosms (Vanni 1987). Then, despite fish were regularly stocked in all lakes from the 1920s, evidences for strong fish predation pressure appeared only from the 1940s when lake nutrient concentration increased and could sustain an important fish population. Therefore, although fish predation pressure exerted a strong structuring effect on cladoceran community structure before 1980, this top-down control was, *in fine*, allowed because of increased lake productivity.

In contrast, from the 1980s, GAMs showed that P concentration was not the only forcing explaining changes in cladoceran communities of all three lakes. Actually, in all three lakes, only *Daphnia* abundance was driven by TP and hence responded to reduced nutrient inputs while the dynamics of all the other cladoceran taxa seemed to be determined by other forcings. Indeed, *Bosmina* 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, decreased TP concentrations in all three lakes did not result in reverse trajectories for the cladoceran communities. Such a failure to 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 these lakes, these trajectories have been attributed to the impact of climate (e.g., Jeppesen et al. 2007, Søndergaard et al. 2007). All three studies lakes have also been undergoing similar warmer air temperature during the last 25 years.

However, results showed that sensitivity to climate change differed between lakes and that climate variability has triggered different responses between systems.

III.5.3. To what extent can climate explain the lack of recovery to pre-eutrophication state?

In Lake Annecy, observed trends in the structure of *Bosmina* and *Daphnia* populations could not be related to any obvious climate warming effects. These conclusions are strengthened by a recent study which showed, from monitoring data, that cladoceran succession pattern in Lake Annecy observed during the 2003 extreme heat wave was not different from the one usually observed over the 1995-2003 time period, in contrast to Lake Geneva (Anneville et al. 2010). The continuous shrinking of *Daphnia* over the last 60 years and the persistence of an abundant *Bosmina* population actually result from a still increasing fish predation pressure on zooplankton, artificially maintained through annual whitefish stocking until 1997. Changes in fish planktivory as a result of fisheries management practices outweigh the impact of global warming in Lake Annecy.

In contrast, GAMs confirmed a significant implication of warming to changes in cladoceran communities in the other two lakes, Geneva and Bourget. They yet showed that the pathways according to which climate has impacted cladoceran communities may partly differ between the two lakes. In both lakes, air temperature was, from the 1980s, a main contributor to PCs scores and the direction of correlations would support a positive effect of warmer temperatures on the abundance of *Bosmina* species, *L. kindti* and *B. longimanus*. These results may support the hypothesis of a direct effect of climate on cladoceran communities through physiological processes. Indeed, *Bosmina* generally presented a faster development and growth than *Daphnia* and warming is expected to even emphasize this gap (Vijverberg 1980). In addition, longer stratification periods should favor the thermophilic taxa as *L. kindti* and *B. longimanus* (Wagner and Benndorf 2007, Manca et al. 2009). In Lake Bourget, GAM did not highlight any clear interaction between climate and local forcings. Hence, this might be the major pathway under which climate has been influencing the pelagic food web. 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 to promote summer bloom of filamentous algae (Paerl and Huisman 2008) and such 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* over *Daphnia* (Gliwicz and Lampert 1990).

In Lake Geneva, the contribution of increased air temperature to PC1 scores was also shown to be coupled and positively related to fish predation pressure from the late 1980s. Such results hence suggest that climate warming might also exert a more indirect structuring effect on cladoceran communities, by increasing the top-down control in this lake. This was highlighted by *Daphnia* size that remained small during re-oligotrophication, with subsequent implications for competition with *Bosmina*. Hence, in Lake Geneva, 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. Such decoupling might be explained by the recovery of whitefish stock in Lake Geneva that was previously attributed to a combination of fisheries management practices and climate effect (Gerdeaux 2004, Anneville et al. 2009). Indeed, whitefish stock recovery has been promoted by higher stocking from the late 1980s to improve whitefish yield (Gerdeaux 2004), and warming more favourable for whitefish recruitment (Eckmann et al. 1988), which intensified the benefit of stocking (Gerdeaux et al. 2006, Anneville et al. 2009).

III.5.4. 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) 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. Similar conclusions were achieved by Cardille et al. (2009) when investigating carbon and water cyclings 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, upstream and downstream connections. Indeed, geomorphological characteristics are thought to modulate lake susceptibility to meteorological forcings, shallow lakes being more sensitive than deeper ones (Georges et al. 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 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. Such lack of sensitivity so far might rather be the consequence of its low nutrient concentration. Consistently, recent phytoplankton changes in Lake Constance, another deep, temperate subalpine lake with similar nutrient status, were shown to be essentially induced by decreased phosphorous concentrations with no evidence of climatic influence (Stich and Brinker 2010). In addition, the analysis of long-term data-series for phytoplankton of five deep temperate subalpine 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 shown to be 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 amongst 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 could also occur along an indirect pathway, involving increased recruitment of zooplanktivorous fish following fisheries management practices. While whitefish stocking has been performed in both lakes, rearing strategies differed, especially from the 1980s. At first, only yolk-sac larvae were released in both lakes. For Lake Bourget, releasing of yolk-sac larvae were halted in 1965 to restart in 1986 with only juveniles (Champigneule et al. 2001). In Lake Geneva, stocking efforts have increased since, in addition to yolk-sac larvae; fingerlings, from the 1980s, and juveniles, from the 1990s, have also been released (Gerdeaux 2004). Therefore, more intensive stocking and the release of different development stages in Lake Geneva, 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.

Acknowledgments

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III.6. Appendix A: Details of coring and chronological analysis on sediment cores, and statistical analyses on abundance of subfossil cladoceran remains.

III.6.1. Coring and chronology

For sediment dating, ^{210}Pb , ^{226}Ra , ^{137}Cs and ^{241}Am activities were measured by gamma spectrometry on cores LEM10P101 (for Lake Geneva), LDB04P1 (for Lake Bourget) at the the Modane underground laboratory (LSM) environmental radioactivity facility (Reyss *et al.*, 1995). Measurements were made on 1–3 g of dried sediments, using high-efficiency, very-low-background, well-type germanium detectors (Reyss *et al.* 1995). Six standards were used to calibrate the gamma detectors (Cazala *et al.* 2003). Generally 24–48 h of counting time were required to reach a statistical error below 10% for excess ^{210}Pb in the deepest samples and for the 1963 peaks of ^{137}Cs and ^{241}Am . The excess ^{210}Pb (i.e., formed in the atmosphere by the decay of ^{222}Rn) was calculated as the difference between the total ^{210}Pb and ^{226}Ra (supported ^{210}Pb) activities. This calculation is based on the assumption that the intermediate daughter product, ^{222}Rn , is in equilibrium with ^{214}Pb (i.e., ^{226}Ra , Arnaud *et al.* 2006). The CFCS model (Constant Flux, Constant Sedimentation, Golberg 1963, Krishnaswami *et al.* 1971) was chosen for this study because sediment rate is dominated by constant sedimentation for recent sediments and because atmospheric flux of radionuclide ^{210}Pb is constant for the two lakes, as shown by the linear radionuclides decrease (Lake Geneva, $R^2=0.924$ and Lake Bourget, $R^2=0.937$; Figure III.4). Whatever the model or procedure used, ^{210}Pb -based chronologies must always be confirmed by independent methods (Smith 2001). Generally, ^{210}Pb dates are confirmed using ^{137}Cs profiles, when the ^{137}Cs profiles are sufficiently intact (Appleby and Oldfieldz 1983).

The $^{210}\text{Pb}_{\text{exc}}$ profiles in the reference cores of Lakes Geneva and Bourget showed a regular and exponential decay in relation to depth. CFCS age modelling indicated an average sedimentation rate of 3.3 mm y^{-1} for Lake Geneva and 4.0 mm y^{-1} for Lake Bourget (Figure III.4). The ^{137}Cs activity versus depth profile showed a small peak at 7.5 and 8.3-cm depth respectively for Lake Geneva and Lake Bourget, without any increase in ^{241}Am activity, corresponding to the fallout from Chernobyl accident in 1986.

This chronological marker implied an average sedimentation rate of 3.4 mm yr⁻¹ for Lake Geneva between 1986-2008 and of 4.4 mm yr⁻¹ for Lake Bourget between 1986-2005. The well-resolved peak of ¹³⁷Cs visible at 13.5 and 17.5-cm for Lake Geneva and Lake Bourget, respectively, coinciding with a peak of ²⁴¹Am, confirmed that sediment at these depths were deposited at the period of maximum artificial radionuclide fallout due to nuclear weapon tests, in 1963. Age-depth relationships corresponded to an average sediment rate of 3.2 mm yr⁻¹ for Lake Geneva between 1963-2008 and of 4.2 mm yr⁻¹ for Lake Bourget between 1963-2005. The good agreement between average sedimentation rates deduced from ²¹⁰Pb_{exc}, ¹³⁷Cs and ²⁴¹Am profiles allowed the extrapolation of the regular sedimentation rate of 3.3 mm yr⁻¹ and 4.2 mm yr⁻¹ giving 164 yr and 183 yr of sedimentation respectively for Lake Geneva and Lake Bourget.

III.6.2. Subfossil cladoceran analysis

To convert the volume-based concentration of remains to weight units [remains (g dry wt)⁻¹], a known volume of wet core sample was weighted, then dried and reweighted. Net accumulation rates (remains cm⁻² year⁻¹) were assessed from concentration of remains per unit weight of dry sediment, sedimentation rate and sediment dry weight per unit volume.

III.6.3. Statistical analyses

Biostratigraphic sequences for cores LEM10_P8, for Lake Geneva; LDB09_P3, for Lake Bourget and 06-03, for Lake Annecy (see Perga et al. 2010) were divided into zones by chronological clustering to facilitate results description. A Bray-Curtis dissimilarity index was computed from the raw data set for each lake; including only abundance of subfossil remains of each taxon with the vegan package (Oksanen et al. 2008) for the R statistical software (<http://www.r-project.org/>). These Bray-Curtis dissimilarity indexes were used for chronologically constrained cluster analysis, based on the method of incremental sum of squares, to reveal the timing of major changes in the cladoceran communities of each sediment core using CONISS in Rioja package (Juggins 2009) for R. The number of statistically different biozones was assessed using the broken-stick approach (Bennett 1996) in Rioja package (Juggins 2009) for R.

Significant changes in the abundance of each taxa between adjacent zones were thereafter tested, using non-parametric tests (Kruskal-Wallis tests accounting for Bonferroni's corrections) to avoid problems related to data heteroscedasticity and non-gaussian distribution.

Principal components analysis (PCA) of remains abundance data after Hellinger transformation (Legendre and Gallagher 2001) was used to explore and summarize patterns of cladoceran community changes over the time period considered for each lake; 1957-2008, 1876-2005 and 1862-2005, for Lake Geneva, Bourget and Annecy respectively. PCA was performed using the ADE4 package (Chessel et al. 2004) for R.

In order to investigate the relationships between the trajectory of cladoceran community and environmental forcing as well as to separate and quantify their influences, a generalized additive model (GAM, Hastie and Tibshirani 1990) was used. GAM is a nonparametric 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 additive sum of unspecified (not linear, not parametric) smooth functions. In this study, the response variable was the scores of the first two PCA axes and the predictors were the proxy of changes in climate, nutrient levels and fish predation pressure detailed previously. The general form of GAM is:

$$y_i = \alpha + \sum f_j(x_{ij}) + \epsilon_i, \quad \epsilon \sim N(0, \sigma^2 \mathbf{\Lambda})$$

where y_i is the link function defining the relationship between the response variable and the additive predictor, α is a constant representing the intercept, f_j s are smooth functions estimated individually for each predictor (x_{ij}) and ϵ the error term. Here, the degree of smoothness of f_j s is controlled through the use of penalized regression spline with smoothing parameters selected by restricted maximum likelihood. A Gaussian distribution with identical link function was used for the error term (ϵ). As the error term is assumed to have a variance matrix $\sigma^2 \mathbf{\Lambda}$ and that the sediment core samples were irregularly distributed in time we used a continuous-time, first-order autoregressive process [CAR(1)] as correlation matrix for $\mathbf{\Lambda}$ (Simpson and Anderson 2009). This GAM-based analysis was performed using the mgcv package (Wood 2006,2011) for R. *P*-values based on likelihood ratio test were used to evaluate the significance of each additional factor.

Automatic selection procedure of model was used to select predictors to be retained in the final model with MuMIn package (Barton 2011) for R. This procedure consists in generating all possible models by combination of the predictors from the saturated model and in classifying these models according to Akaike's Information Criterion (AIC). A manual stepwise selection procedure – in which, at each loop, the predictor responsible for the lowest AIC reduction was dropped – was used to validate the best model.

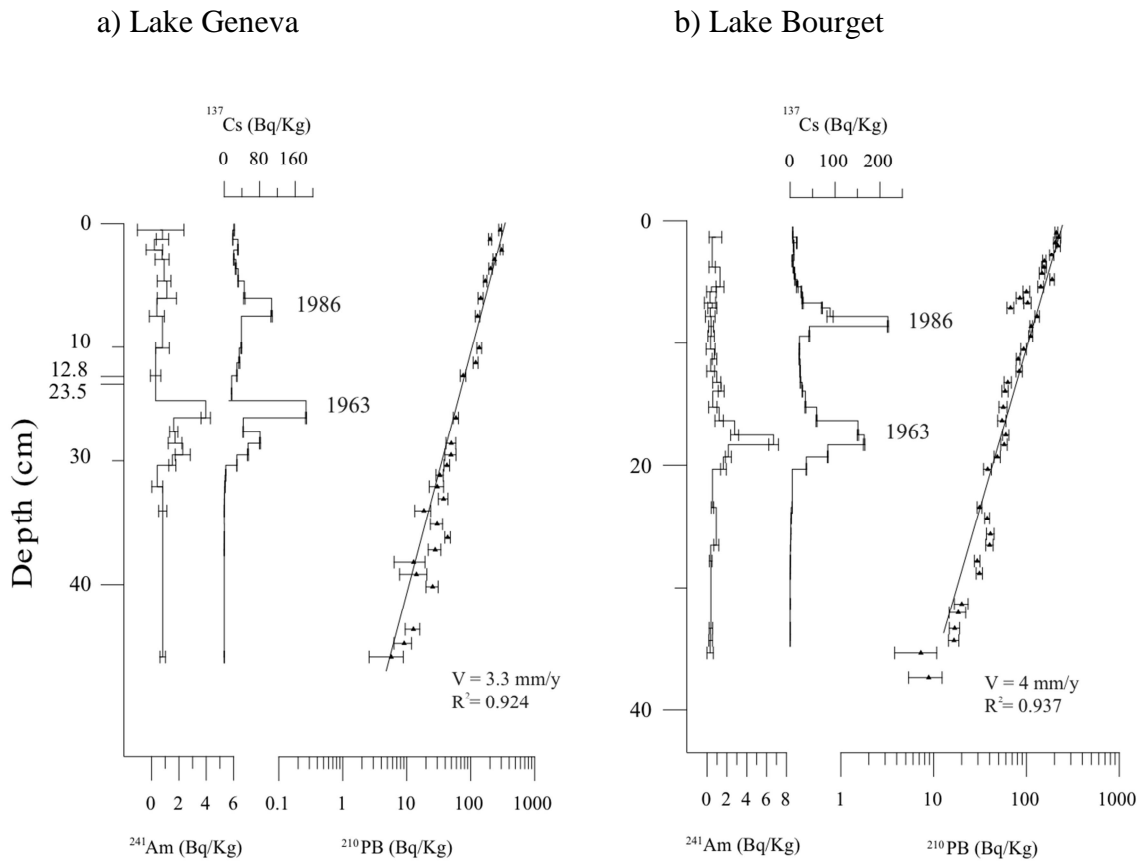


Figure III.4. Age-depth model of (a) Lake Geneva (sediment core LEM10_P101) and (b) Lake Bourget (sediment core LDB04_P1) from radionuclides (^{137}Cs , ^{241}Am and ^{210}Pb).

III.7. Appendix B: Results of Kruskal-Wallis tests accounting for Bonferroni's corrections on abundance of cladoceran remains.

Table III.2. Temporal changes in the abundance of cladoceran taxa in Lake Annecy. Kruskal-Wallis tests accounting for Bonferroni's corrections. Zones (A-Z1 to A-Z4) correspond to major changes in the cladoceran community determined by chronological clustering analysis (see figure 2 for more details).

<i>Daphnia</i> sp.			
	A-Z1	A-Z2	A-Z3
A-Z2	1.000		
A-Z3	8.60×10^{-5}	0.003	
A-Z4	2.40×10^{-7}	7.20×10^{-4}	0.106
<i>E. longispina</i>			
	A-Z1	A-Z2	A-Z3
A-Z2	0.001		
A-Z3	7.00×10^{-5}	0.274	
A-Z4	3.10×10^{-8}	5.00×10^{-4}	0.003
<i>B. longirostris</i>			
	A-Z1	A-Z2	A-Z3
A-Z2	0.001		
A-Z3	4.60×10^{-5}	0.002	
A-Z4	4.60×10^{-11}	3.80×10^{-9}	0.014
<i>S. crystallina</i>			
	A-Z1	A-Z2	A-Z3
A-Z2	0.004		
A-Z3	2.30×10^{-6}	0.0013	
A-Z4	0.353	0.071	2.10×10^{-7}

Table III.3. Temporal changes in the abundance of cladoceran taxa in Lake Geneva. Kruskal-Wallis tests accounting for Bonferroni's corrections. Zones (L-Z1 to L-Z5) correspond to major changes in the cladoceran community determined by chronological clustering analysis (see figure 2 for more details).

<i>Daphnia</i> sp.				
	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	0.005			
L-Z3	4.10×10^{-4}	0.324		
L-Z4	0.281	0.153	0.001	
L-Z5	5.40×10^{-6}	7.90×10^{-8}	1.90×10^{-9}	1.80×10^{-4}
<i>E. longispina</i>				
	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	0.281			
L-Z3	1.000	0.059		
L-Z4	0.454	0.032	0.142	
L-Z5	1.000	0.009	1.000	0.009
<i>E. coregoni</i>				
	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	0.790			
L-Z3	0.122	0.001		
L-Z4	0.508	0.036	1.000	
L-Z5	1.50×10^{-5}	1.30×10^{-7}	0.002	0.002
<i>B. longirostris</i>				
	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	1.000			
L-Z3	1.000	1.000		
L-Z4	0.021	0.004	0.001	
L-Z5	0.018	0.054	0.053	9.50×10^{-5}
Chydoridae				
	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	1.000			
L-Z3	1.000	1.000		
L-Z4	1.000	0.332	0.015	
L-Z5	1.000	1.000	1.000	0.003
<i>B. longimanus</i>				
	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	1.000			
L-Z3	1.000	1.000		
L-Z4	0.710	1.000	1.000	
L-Z5	0.002	2.80×10^{-5}	2.00×10^{-7}	0.047

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S. crystallina

	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	1.000			
L-Z3	0.040	0.023		
L-Z4	0.007	0.002	0.001	
L-Z5	5.30×10^{-6}	7.80×10^{-8}	1.90×10^{-9}	1.000

L. kindtii

	L-Z1	L-Z2	L-Z3	L-Z4
L-Z2	0.005			
L-Z3	0.002	0.103		
L-Z4	0.008	0.003	0.001	
L-Z5	2.00×10^{-6}	2.70×10^{-8}	6.30×10^{-10}	1.80×10^{-4}

Table III.4. Temporal changes in the abundance of cladoceran taxa in Lake Bourget. Kruskal-Wallis tests accounting for Bonferroni's corrections. Zones (B-Z1 to B-Z5) correspond to major changes in the cladoceran community determined by chronological clustering analysis (see figure 2 for more details).

<i>Daphnia</i> sp.				
	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	8.20 x 10 ⁻⁴			
B-Z3	0.001	1.000		
B-Z4	0.004	1.000	1.000	
B-Z5	4.90 x 10 ⁻⁵	2.20 x 10 ⁻⁵	4.80 x 10 ⁻⁵	5.20 x 10 ⁻⁶
<i>E. longispina</i>				
	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	0.058			
B-Z3	0.101	1.000		
B-Z4	1.000	0.026	0.048	
B-Z5	1.000	0.009	0.008	1.000
<i>E. coregoni</i>				
	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	0.256			
B-Z3	1.000	1.000		
B-Z4	0.064	0.001	0.017	
B-Z5	8.60 x 10 ⁻⁵	2.00 x 10 ⁻⁵	4.40 x 10 ⁻⁵	0.056
<i>B. longirostris</i>				
	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	0.031			
B-Z3	0.022	0.010		
B-Z4	0.370	1.000	0.006	
B-Z5	3.60 x 10 ⁻⁵	2.00 x 10 ⁻⁴	5.70 x 10 ⁻⁵	3.10 x 10 ⁻⁵
Chydoridae				
	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	1.000			
B-Z3	1.000	1.000		
B-Z4	0.045	0.005	0.070	
B-Z5	0.006	7.20 x 10 ⁻⁴	0.045	1.000
<i>B. longimanus</i>				
	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	0.488			
B-Z3	0.006	0.053		
B-Z4	0.006	0.053	1.000	
B-Z5	0.002	0.054	0.383	1.000

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S. crystallina

	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	1.000			
B-Z3	0.400	1.000		
B-Z4	1.000	1.000	0.63	
B-Z5	2.20×10^{-5}	1.90×10^{-5}	4.00×10^{-5}	7.80×10^{-6}

L. kindtii

	B-Z1	B-Z2	B-Z3	B-Z4
B-Z2	0.003			
B-Z3	0.001	1.000		
B-Z4	1.50×10^{-4}	0.017	0.119	
B-Z5	4.70×10^{-8}	1.80×10^{-5}	2.50×10^{-4}	0.469

III.8. Appendix C: Contribution of various covariates to the final GAMs fitted to cladoceran PC1 and 2 scores for each lake.

Table III.5. Summary for the final GAMs fitted to cladoceran PC1 scores for each lake. Covariates are arranged in ascending order of their contribution to the final GAMs.

Lake	Covariate	PC1				Res. dev. (% expl.)
		edf	Res. df	<i>F</i>	<i>P</i>	
Geneva	Predation pressure	2.42	3.01	5.28	0.004	67.8
	Annual air temperature	1.79	2.19	5.60	0.006	
	Phosphorous	3.06	3.78	3.44	0.018	
	Explained deviance (%)					
Bourget	Annual air temperature	2.86	3.59	13.93	1.06×10^{-7}	79.1
	Phosphorous	4.93	6.04	5.49	1.31×10^{-4}	
	Predation pressure	1.00	1.00	6.87	0.011	
	Explained deviance (%)					
Annecy	Predation pressure	2.92	3.00	19.66	3.83×10^{-9}	69.8
	Phosphorous	1.00	1.00	9.74	0.003	
	Explained deviance (%)					

edf, effective degrees of freedom for the regression spline; Res. df, reference degrees of freedom used to compute the *P*; *F*, F-statistic; *P*, associated probabilities; Res. dev. (% expl.), deviance is a measure of residual variation around the final GAM models analogous to the sum of square in linear regression.

Table III.6. Summary for the final GAMs fitted to cladoceran PC2 scores for each lake. Covariates are arranged in ascending order of their contribution to the final GAMs.

Lake	Covariate	PC2				Res. dev. (% expl.)
		edf	Res. df	<i>F</i>	<i>P</i>	
Geneva	Phosphorous	4.38	5.32	15.83	7.56×10^{-9}	72.5
	Predation pressure	2.11	2.64	3.84	0.020	
	Explained deviance (%)					
Bourget	Phosphorous	2.59	3.26	6.41	5.21×10^{-4}	37.7
	Annual air temperature	2.22	2.81	3.51	0.022	
	Predation pressure	1.26	1.47	3.45	0.041	
	Explained deviance (%)					

edf, effective degrees of freedom for the regression spline; Res. df, reference degrees of freedom used to compute the *P*; *F*, F-statistic; *P*, associated probabilities; Res. dev. (% expl.), deviance is a measure of residual variation around the final GAM models analogous to the sum of square in linear regression.

IV. Hybridation interspécifique et perturbations multiples

Long-term changes in *Daphnia* reproductive behaviour in three large deep lakes.

En préparation

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IV.1. Abstract

Environmental changes have been shown to affect the physiological and phenological characteristics of biological communities, such as their trophic interactions, but their potential impacts on species reproductive strategies have rarely been considered. Herein, we investigated the relative roles of climate warming and local forcings (changes in nutrient inputs and fish predation pressure) on the reproductive strategies and subsequent hybridization events in the *Daphnia cucullata-galeata-longispina* species complex over long time scales, through the genetic analysis of *Daphnia* ephippia archived in sediment of three large deep lakes. First, invasion from southern to northern lakes by *D. galeata* with subsequent interspecific hybridization events is not a generality since *D. galeata* was shown to be present in lakes Geneva and Bourget before eutrophication. We show that the settlement and maintenance of *D. galeata* requires at least a mesotrophic status since no *D. galeata* ephippia were found in Lake Annecy. In addition, local forcings (i.e., eutrophication and fish predation pressure) and climate warming could induce a synchronization of reproductive timing between *D. galeata* and *D. longispina*, resulting in subsequent hybridization events in Lakes Geneva and Bourget. Environmental forcing could act in two ways. Crowding related to eutrophication was thought to be a trigger of simultaneously sexual reproduction for *D. galeata* and *D. longispina*, while fish predation pressure and climate warming were thought to disrupt the timing of sexual reproduction of *D. galeata* increasing the probability of encounter between the sexual stages of *D. galeata* and *D. longispina*. In addition, the persistence of hybridization events in spite of re-oligotrophication period in Lake Bourget highlighted that other environmental forcings than trophic status, such as climate warming, can influence the reproductive timing of *Daphnia* in large deep lakes. Finally, our results indicated that directionality of hybridization can be driven by a complex combination of interacting mechanisms (i.e., reproductive behaviour of males, timing of occurrence of sexual stages and unbalanced sexual stages production among syntopic species).

IV.2. Introduction

So far, the assessment of ecosystems vulnerability to anthropogenic forcings has been primarily done using criteria related to community ecology (e.g., Stenseth et al. 2002, Walther et al. 2002). Attention is usually focussed on how environmental changes affect the communities' composition through modifications of their habitats, growth, mortality, phenology as well as their trophic interactions (Sommer et al. 1986, Moore et al. 1996, Walther et al. 2002). Yet, many taxonomic groups can adjust their reproductive strategies to environmental conditions (Hebert 1987). Hence, anthropogenic forcings might trigger, for such taxa, changes in reproductive strategies, with potentially far reaching consequences for population dynamics and species composition, although these have been poorly studied so far.

In cyclically parthenogenetic organisms such as many cladocera, population maintenance is based on the balance between clonal multiplication and sexual reproduction (Berg 1934, Hebert 1980). In general, for *Daphnia*, parthenogenesis occurs for most of the year whereas the induction of sexual reproduction is restricted to distinct periods when environmental conditions deteriorate (Hebert 1978). Sexual reproduction results in the production of males and haploid eggs which need to be fertilized (Hebert 1978). Fertilized sexual eggs are resting eggs encased in a resistant structure called ephippium (Schultz 1977). Ephippia production allows first *Daphnia* to avoid deleterious conditions either by an escape in space (via dispersal), or in time (via diapause) (Gyllström and Hansson 2004). In addition, ephippia constitute a reservoir of recombined genotypes on which natural selection can operate (Brendonck and De Meester 2003).

Sexual reproduction requires the production of both males and sexual females and only half of an individual's genome is transmitted to the offspring. Sexual reproduction thus implies higher direct evolutionary and energetic costs than clonal multiplication (Williams 1975, Maynard Smith 1978). Theoretically, the stability, predictability or frequency of periods of harsh environmental conditions coupled with the costs of the defence induction determines whether sexual reproduction is a viable strategy or not (Harvell 1990, Gyllström and Hansson 2004). Therefore, it is likely that sexual activity and subsequent diapause will differ between habitats of different stability, as shown for temporary and permanent ponds.

Initially, diapause was first associated with habitats with large seasonal fluctuations in environmental conditions, such as temporary ponds that can dry or freeze to the bottom every year (Hebert 1978). In these habitats, the advantage of diapause is fairly obvious since active populations would be wiped out by such events (Hebert 1978). Diapause has, however, been shown to be also important in large permanent lakes (Hairston and Van Brunt 1994, Weider et al. 1997).

A number of natural stimuli that induce sexual reproduction in *Daphnia* have been proposed, including temperature, photoperiod and crowding (Stroos and Hill 1965, Hobaek and Larsson 1990, Kleiven et al. 1992) as well as changes in food levels (Carvalho and Hughes 1983, LaMontagne and McCauley 2001, Alekseev and Lampert 2001) and intensity of predation pressure (Pijanowska and Stolpe 1996, Slusarczyk 2001), all being characteristics that can be altered by most human-driven perturbations undergone by lakes over the last decades, such as changes in nutrient loadings, modified fish communities or climate change. Human forcings might have hence affected the triggers of *Daphnia* sexual reproduction over time.

The existence of resting egg banks in lake sediment has already offered the opportunity to reconstruct changes in past population structures (e.g., Yan et al. 1996, Pollard et al. 2003, Mergeay et al. 2004), in genetic architecture (e.g., Weider et al. 1997, Brede et al. 2009, Rellstab et al. 2011), and microevolutionary trajectories (e.g., Hairston et al. 1999, Kerfoot et al. 1999, Cousyn et al. 2001) in response to environmental perturbations. The nature of triggers of hybridization events has rarely been investigated over the long term. In this work, genetic analysis of *Daphnia ephippia* archived in sediments was performed in order to determine whether climate warming and local forcings (eutrophication/re-oligotrophication and changes in management practices) have induced changes in the timing and frequency of sexual reproduction, hybridizations and introgression between taxa constituting the *Daphnia cucullata-galeata-longispina* species complex (*D. longispina* formerly known as *D. hyalina*, see Petrusek et al. 2008) in three large deep lakes over the last century. In general, the presence of pre- and/or post-mating barriers between co-existing species might limit interspecific hybridization (Spaak 1995, Schwenk et al. 2001). The temporal and spatial scales in the induction of males and females of syntopic species may be important pre-mating barrier for hybridization events (Spaak et al. 2004). Therefore, we suppose that the appearance of hybridization events at a given time period would be related to environmental conditions which alter the timing of sexual reproduction resulting in a decrease of mating barrier.

Directionality of hybridization (i.e., whether a species acts more frequently as male or female) has also been addressed since it provides deeper insights on the reproductive behaviour of different *Daphnia* species.

IV.3. Material and methods

IV.3.1. Study sites

Lakes Geneva, Bourget and Annecy are warm-monomictic lakes situated in the northwestern edge of the French Alps. They are the largest lakes in France with surface areas of 582, 42 and 27 km² and maximum depths of 309, 145 and 69 m for Lake Geneva, Bourget and Annecy respectively. Lakes trophic histories have been documented by previous paleolimnological studies (Giguet-Covex et al. 2010, Perga et al. 2010, Alric et al. submitted) along with ongoing monitoring surveys (INRA long-term observatory database). Increasing human pressure during the economic development initiated in the 1930-1940's led to a dramatic increase in the phosphorous load in all three lakes. However, although these lakes are in a geographical vicinity (located in a radius of 35 km), the extent of eutrophication differed among them. In Lake Annecy, the early implementation of restoration measures as soon as 1967 limited the eutrophication level. After that the maximum lake total phosphorous concentration ([TP]) was <20 µgP L⁻¹ (oligo-mesotrophic status, Perga et al. 2010) in the late 1960's, lake [TP] has been gradually decreasing and is now <6 µgP L⁻¹. For Lakes Geneva and Bourget, nutrient abatement strategies were lagging behind and started only in the 1970s-early 80s, while lakes had already switched to a settled eutrophic status (max [TP] were 90 and 130 µgP L⁻¹ for Lake Geneva and Bourget respectively). Following the restorations programs [TP] has been successfully reduced over the last 30 years to levels more typical for oligo-mesotrophic lakes (23 and 17 µgP L⁻¹ for Lake Geneva and Bourget respectively in 2010; INRA long-term observatory database).

IV.3.2. Pelagic Daphnia from Lake Geneva

In order to better evaluate which kind of information might be retrieved from genetic analyses on resting eggs, we conducted a preliminary experiment in which we compared the genetic structure of parthenogenetic and sexual females for a one year survey in Lake Geneva. Zooplankton was sampled weekly to monthly from January to December 2011 in Lake Geneva by two vertical hauls from a depth of 50 m to the surface using a 200- μ m mesh conical net, at the lake deepest point. One vertical haul was designated for *Daphnia* counting (INRA long-term observatory database) and the other for genetic analyses on *Daphnia*. Genetic analyses were performed only for time periods where abundance peaks were observed, period of potential sexual reproduction. Four dates were chose (2 and 30 May 2011 and 21 and 28 June 2011) for which 20-30 asexual females and 16 sexual females with a minimum body size of 1 mm were randomly selected for future genetic analyses, excepted for the last time period (28 September 2011) where only asexual females were found.

IV.3.3. Coring and chronology

In total, 24 sediment cores were collected in 2010 (for Lakes Geneva and Bourget) and 2011 (for Lake Annecy) using a quadruple gravity corer (UWITEC, Mondsee, Austria) from the deepest point of the respective lake (eight cores for each lake). For each lake, dating of sediment cores from which *Daphnia* ephippia were extracted was done by correlation to a reference core using lithological tie points. Details on the dating of the reference cores can be found in Perga et al. (2010) and Alric et al. (submitted). Briefly, sediment dating was performed using gamma spectrometry (measurement of ^{210}Pb , ^{226}Ra , ^{137}Cs and ^{241}Am activities) at the Modane underground laboratory (LSM) environmental radioactivity facility (Reyss et al. 1995). To obtain a sufficient number of *Daphnia* ephippia and resting eggs for each lake, we pooled sediment layers covering, on average 18 years (range: 8-41 years), 11 years (range: 5-31 years) and 22 years (range: 10-50 years) for Lake Geneva, Bourget and Annecy respectively. *Daphnia* ephippia were isolated by stirring sediment in distilled water and sieving through a 100- μ m mesh size filter-cup.

IV.3.4. Genetic analysis

Daphnia ephippia were manually opened under a binocular and embryos were isolated and placed individually into 0.2 mL tubes for DNA extraction using the hot sodium hydroxide and Tris method (HotSHOT) according to Montero-Pau et al. (2008). Two types of genetic markers were used for each individual: a mitochondrial DNA (mtDNA) marker and nuclear microsatellites. Discrimination between *D. galeata* and *D. longispina* mitochondrial genotypes was performed using Restriction Fragment Length Polymorphism (RFLP) after Polymerase Chain Reactions (PCR) amplification of mtDNA (Schwenk et al 1998). The mitochondrial 16S ribosomal subunit DNA was amplified using conserved primers: S1 (5'-CGG CCG CCT GTT TAT CAA AAA CAT-3') and S2 (5'-GGA GCT CCG GTT TGA ACT CAG ATC-3') following Schwenk et al. (1998). Single PCRs were performed with 2 µL of DNA template in a 14 µL reaction volume containing 2 mM MgCl₂, 1 x PCR reaction buffer (20mM Tris-HCl, pH 8.0), 0.25 mM dNTP, 0.5 µM each primer (S1, S2) and 1 U of *Taq* DNA Polymerase (TAKARA BIO INC., Japan). Cycling conditions started with one cycle of 2.5 min at 93 °C, 1 min at 55 °C and 2 min at 72 °C, followed by 40 cycles of 1 min at 93 °C, 1 min at 55 °C and 2 min at 72 °C. The presence of products (≈ 560 base pairs in length) was checked using standard gel electrophoreses on 2% agarose gels ethidium bromide staining (Sambrook et al. 1989). Following PCR amplification, RFLP analyses were performed by single digests of 3.5 µL of PCR products each with three different enzymes, *Dde I*, *Mnl I* and *Rsa I* (all New England BioLabs) for 2.5 h at 37 °C in a total reaction volume of 4.5 µL containing 1 x NEBuffer, 0.8 U of the restriction enzyme, and autoclaved dH₂O, plus 1 x Bovine Serum Albumin only for *Mnl I*. Digested products were separated on 2.5% NuSieve® 3-1 Agarose gels (Lonza) for 3-4 h at 50 V. For present asexual females, the same DNA extraction, PCR and RFLP conditions were used on whole individuals.

Microsatellite analyses were based on eight polymorphic loci: Dp512, SwiD1, SwiD5, SwiD10, SwiD12, SwiD14, SwiD15, Da10/14 (Brede et al. 2006). All loci were combined in one multiplex PCRs performed in 0.2 mL tubes with 11.5 µL reaction volume containing 1.5 mM MgCl₂, 1 x PCR reaction buffer, 0.2 mM dNTP, 1 U of HotStart *Taq* DNA Polymerase (Qiagen) and 1 µL of DNA template. The primer concentrations were of 0.3 µM for SwiD1, SwiD10, Swid15 and Da10/14; 0.4 µM for Swid5 and SwiD14; and 0.5 µM for Dp512.

Cycling conditions started with a 15 min initial denaturation of the template DNA and HotStart *Taq* DNA Polymerase activation step at 95 °C, followed by 32 cycles of 0.5 min at 94 °C, 1.5 min at 54 °C and 1 min at 72 °C and a final extension step of 30 min at 60°C. PCR products were analysed on an ABI 3700 capillary sequencer using a LIZ 500 labelled size standard. Allele scoring was done using GeneMapper 3.7 software (Applied Biosystems).

In order to assign genotypes to certain taxa an additional set of 24 *D. galeata* and 15 *D. longispina* laboratory clones originating from 19 European lakes was used as reference (see Appendix A for more details).

IV.3.5. Data analysis

To infer the population structure of *Daphnia* resting eggs in the three lakes, we applied two different methods using the genetic relatedness of resting eggs determined by allelic variation at eight microsatellite loci. First, factorial correspondance analyses (FCA) were performed on data sets including reference clones and resting eggs for each lake separately using Genetix 4.05 (Belkhir et al. 1996-2004). Second, all microsatellite data were pooled in a single data set and analysed using the program STRUCTURE 2.3.1 in order to estimate the most likely number of clusters and to check the occurrence of hybrids (Pritchard et al. 2000, Falush et al. 2003). This software implements a Bayesian assignment approach dedicated to the quantification of hybridization events from individual multilocus genotypes to estimate posterior probability that an individual belongs to a certain class. The number of clusters tested ranged from K=1 to K=21, with 20 independent runs carried out for each K value. For each run, 10⁵ iterations were carried out after a burn-in of length 10⁵ interactions. Analyses were performed without prior assumptions of population membership; admixture model; α inferred with an initial value of 1, a maximum value of 10, a uniform prior, and the same value for all population; different values of Fst for different subpopulations; a prior mean Fst of 0.01; a prior SD of 0.05; and constant λ with a value of 1. The choice of K was based on the second order rate of change of likelihood (Evanno et al. 2005). Finally, gene flow and mitochondrial introgression were revealed by comparison between microsatellite and mitochondrial data.

IV.4. Results

IV.4.1. *Modern Daphnia populations*

In Lake Geneva, the density of *Daphnia* showed a significant temporal dynamics with a bimodal shape peaking firstly in late spring and early summer and then in fall (Figure IV.1). The density of *Daphnia* was maximum in late spring and early summer. Parthenogenetic and sexual females were found during the first three abundance peaks while only parthenogenetic females were found during the abundance peak in fall. Mitochondrial 16S-RFLP analyses of on parthenogenetic and sexual females revealed three restriction patterns corresponding to three different genotypes, two identified as *D. longispina* (L1, L2) and one as *D. galeata*. The spring abundance peaks were highly dominated by *D. galeata* which contributed from 76% to 100% to the total abundance while the fall peak was exclusively composed of *D. longispina* and the contribution of L1 and L2 to the total sample was 94% and 6% respectively. Although the three haplotypes were found in parthenogenetic females in different contributions to the total samples among to the time period, only one haplotype (*D. galeata*) was found in sexual females (Figure IV.1).

IV.4.2. *Species contribution to resting egg banks in the three lakes*

Based on allelic variation at eight microsatellite loci, *D. galeata* and *D. hyalina* reference clones were separated into two distinct clusters in the FCA analyses (Figure IV.2). The first two axes accounted for 18, 19 and 20% of the total variation in taxonomic composition of resting egg banks in Lake Geneva, Bourget and Annecy, respectively. *D. galeata* and *D. longispina* were separated along axis 1 while axis 2 accounted for the variation within the taxa. Overall, three genotype patterns, i.e. *D. galeata*-like genotypes, *D. longispina*-like genotypes and intermediate genotypes, were identified in the resting eggs retrieved from the sediment cores. In STRUCTURE, resting eggs were also assigned to three groups, i.e. two parental species and hybrids (Figure IV.3).

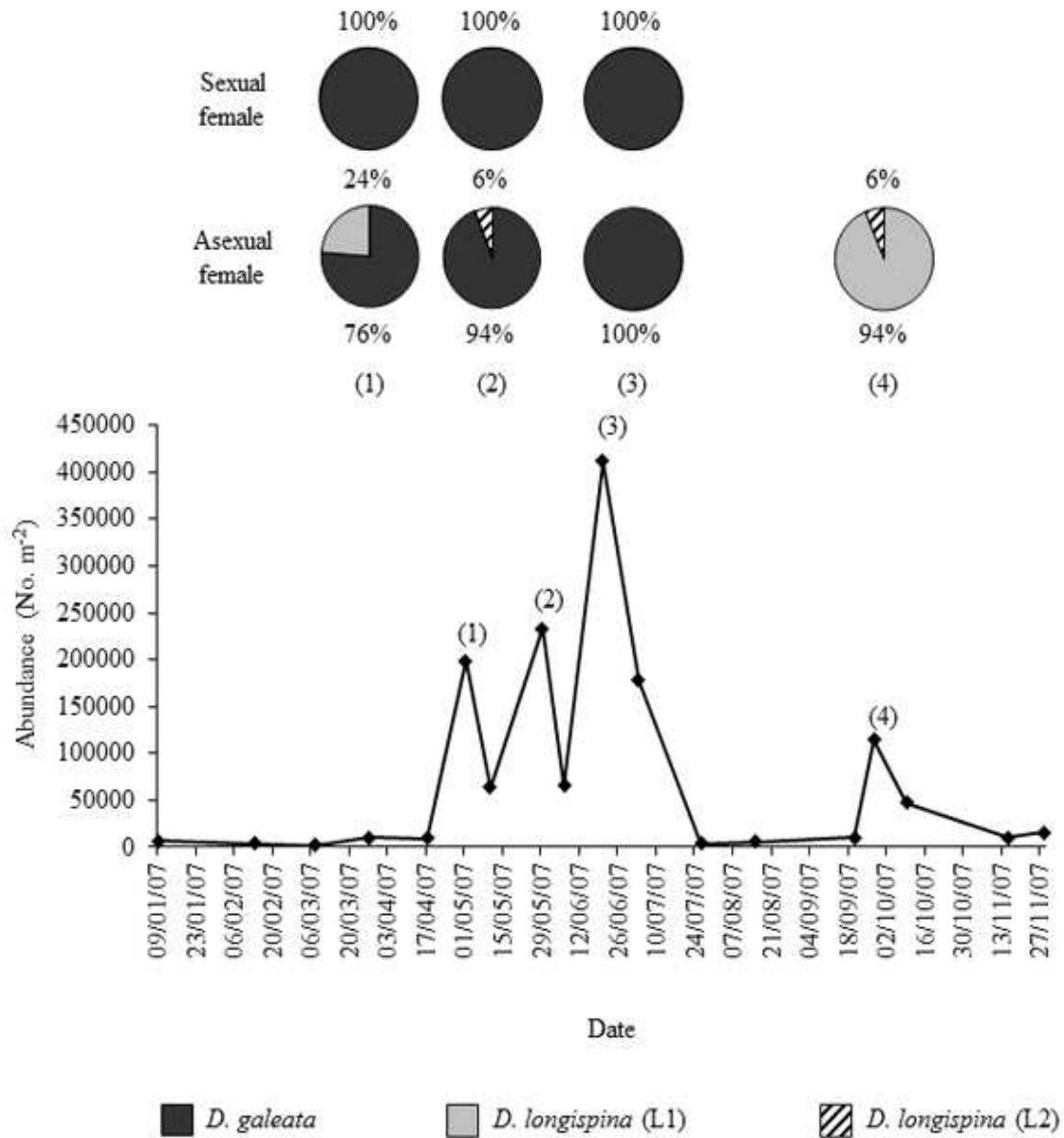


Figure IV.1. Seasonal changes in *Daphnia* abundance in Lake Geneva. Pie diagrams represent the contribution of parental taxa in asexual and sexual females. Parental taxa were identified according to mitochondrial 16S-RFLP (see material and method for more details). In Pie diagrams, gray = *D. longispina* (L1), hatch = *D. longispina* (L2), and black = *D. galeata* (see results for more details).

Taxa assignments by STRUCTURE and FCA clustering were well in correspondence since all resting eggs presenting *D. galeata*-like genotypes or *D. longispina*-like genotypes in the FCA were classified respectively in a single parental species group in STRUCTURE, while intermediate genotypes in the FCA corresponded to the hybrid group in STRUCTURE.

In addition, temporal changes in the contribution of different taxa to sexual reproduction in the three lakes were consistent between FCA and STRUCTURE analysis (Figure IV.2, Figure IV.3). All three identified genotype clusters were found in Lakes Geneva and Bourget while only one (*D. longispina*) was found in Lake Annecy over the whole time period investigated. Furthermore, mitochondrial 16S-RFLP revealed that *D. longispina*, indentified by microsatellite analysis, was constituted by two mitochondrial haplotypes (L1, L2), which were present in all three lakes (Figure IV.3a).

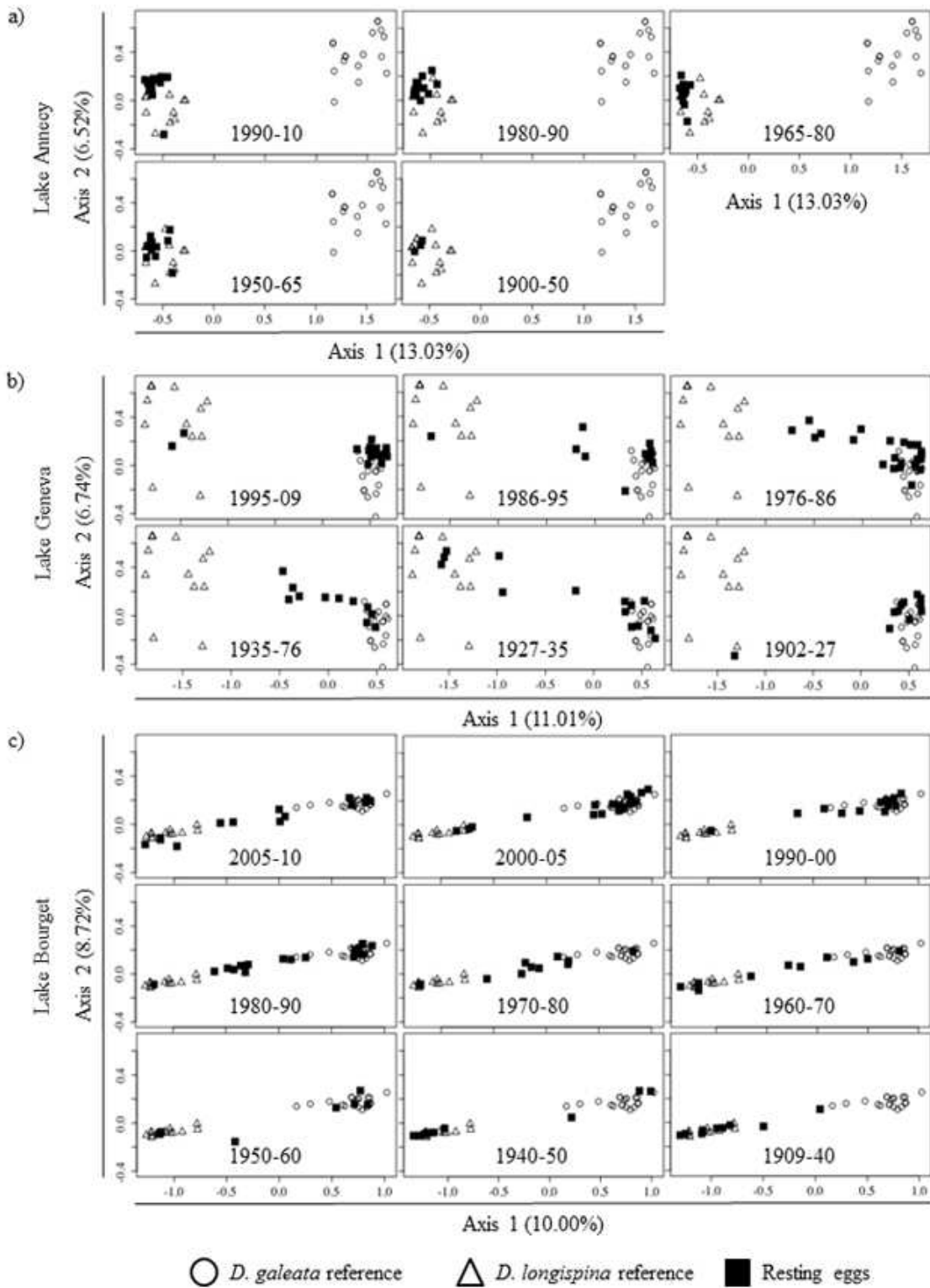
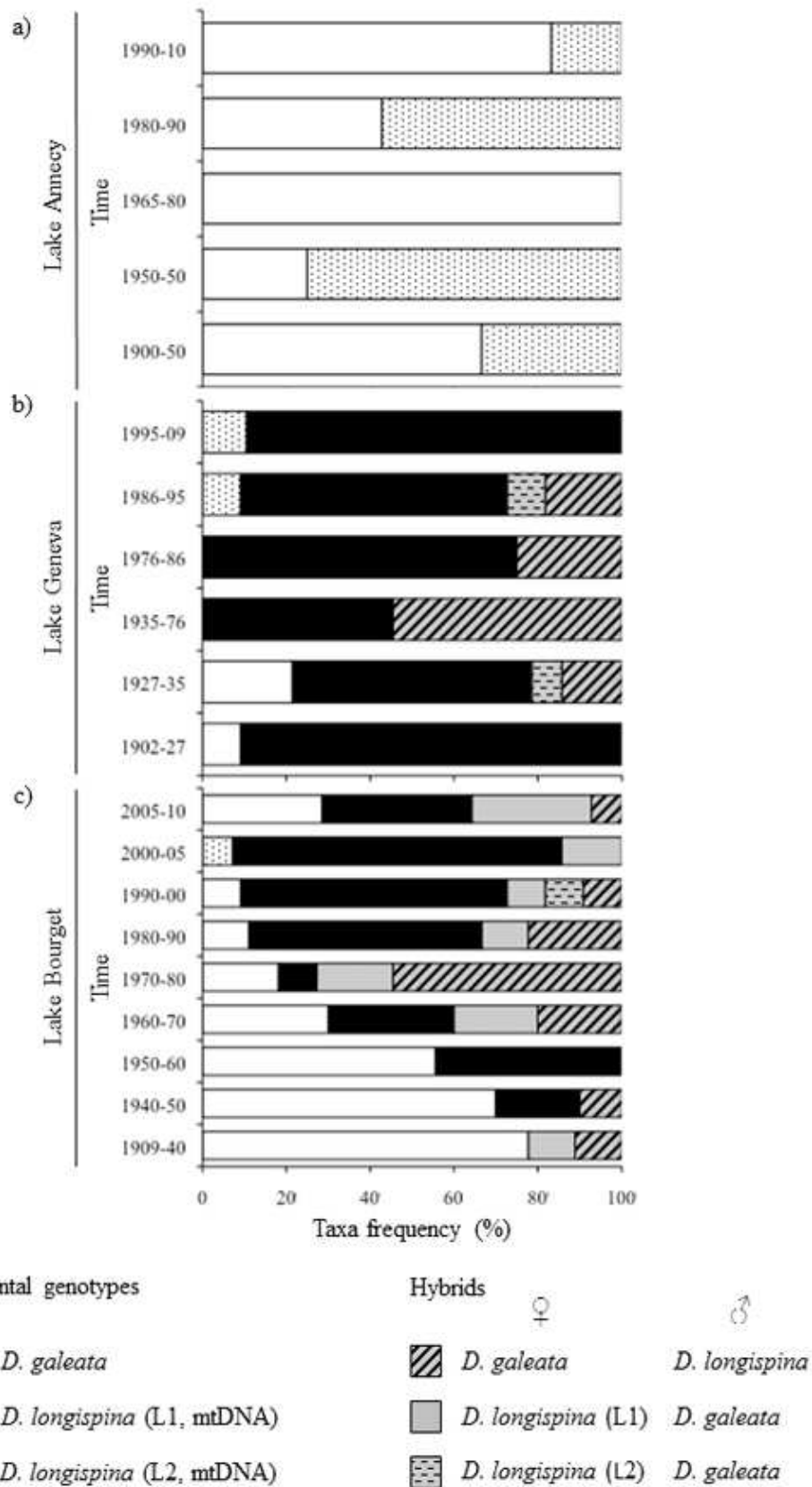


Figure IV.2. Factorial correspondance analysis showing the temporal changes in the resting egg banks in (a) Lake Annecy, (b) Lake Geneva and (c) Lake Bourget based on microsatellite data. References clones from *D. galeata* and *D. longispina* are also included in the analysis.

In Lake Annecy, haplotypes L1 and L2 were found for all studied time periods except for the one covering the mid-1960s to 1970s (corresponding to the maximum eutrophication period) where only L1 was present. In contrast, in Lakes Geneva and Bourget, L1 was the only mitochondrial haplotype of *D. longispina* in resting egg banks before the 1940s (corresponding to the pre-eutrophication period). Its contribution to resting egg banks has been decreasing from the 1940's (early eutrophication) in both lakes (from 21% in the 1930s to 0% in the early 2000s for Lake Geneva and from 78% before the 1940s to 29% in the early 2000s as depicted in Figure IV.3b and c), while L2 appeared in the resting egg banks after the 1980s only (corresponding to re-oligotrophication period). The eutrophication period was also marked by an increased contribution of hybrids to resting egg banks in Lakes Geneva and Bourget with maximum values of 55% between 1935-1976 for Lake Geneva and 73% between 1970-1980 for Lake Bourget (Figure IV.3b,c).

IV.4.3. Past mitochondrial introgression

The combination of microsatellite and mitochondrial data showed a bidirectional hybridization in Lakes Geneva and Bourget as well as differences in the level of mitochondrial introgression among the two lakes (Figure IV.3). Although, in both lakes *D. galeata* was inferred to be the maternal haplotype of *D. galeata* x *D. longispina* hybrids in most cases, its contribution was in different magnitude, on average 89% for Lake Geneva and 52% for Lake Bourget. In Lake Bourget, L1 and L2 were also shown to be the maternal haplotypes of *D. galeata* x *D. longispina* hybrids with a greater contribution of L1 (93%). Conversely, in Lake Geneva only L2 was inferred as the maternal haplotypes of hybrids, even when no ephippia of L2 parental species were found in sediment, such as in the 1930s.



←

Figure IV.3. Temporal changes in species contribution to the resting egg banks and directionality of hybridization in (a) Lake Annecy, (b) Lake Bourget and (c) Lake Geneva. Species and hybrids identification was based on allelic variation at 8 microsatellite loci and STRUCTURE assignment ($K = 2$) and mitochondrial 16S-RFLP (*D. longispina* haplotypes L1 and L2). Directionality of hybridization was based on comparison of microsatellite and mitochondrial markers. Symbols ♂ and ♀ correspond to *Daphnia* species inferred respectively as maternal and paternal haplotype of hybrids by mitochondrial marker.

IV.5. Discussion

IV.5.1. Interpretation of resting eggs bank structure

Sedimentary cladoceran remains are increasingly used, alone or in combination with other paleo-indicators, to evaluate lake responses to environmental perturbations (e.g., Jeppesen et al. 2001, Korhola and Rautio 2001, Amsinck et al. 2007). The majority of studies conducted so far have been based on morphological identification and counting of various exoskeleton remains (e.g., Salo et al. 1989, Manca and Comoli 1995, Chen et al. 2011) whereas only a few have used ephippia (see Amsinck et al. 2007). Moreover, these studies are based on the assumption that sedimentary egg banks really reflect past population abundance and taxonomic composition. However, not all *Daphnia* taxa invest equally into sexual reproduction and hence in the production of ephippia (Cáceres 1998, Jankowski and Straile 2003, Keller and Spaak 2004). Indeed, mitochondrial 16S-RFLP of present pelagic *Daphnia* population in Lake Geneva showed that although parthenogenetic females were from both *D. galeata* and *D. longispina* species, only *D. galeata* performed sexual reproduction during the study year. Hence, the taxonomic composition of ephippia retrieved from large lakes sediment might not necessarily provide a reliable picture of the taxonomic structure of past *Daphnia* populations. However, it can be highly informative regarding taxa that invested in sexual reproduction and can then document changes in *Daphnia* reproductive strategies over time.

IV.5.2. Historical presence of *D. galeata* and *D. hyalina* in the three lakes

Ecological niche of *Daphnia* species may be a natural boundary for dispersal (Flößner and Kraus 1986). Anthropogenic perturbations can, however, modify ecological niches in a lake favouring the establishment of *Daphnia* species which can disrupt the reproductive strategy of the native species with subsequent hybridization events. Eutrophication is considered as such, since it was shown to facilitate the establishment of *D. galeata* in subalpine lakes of north of the Alps (Weider et al. 1997, Jankoswki and Straile 2003, Brede et al. 2009, Rellstab et al. 2011). Recently, a comparison of 43 lakes of Alps along the North-South environmental gradient showed that *D. longispina* is predominantly found in northern large cold oligotrophic lakes whereas *D. galeata* dominated more productive southern lakes (Keller et al. 2008). These observations suggest that eutrophication increased the potential distribution area of *D. galeata*, facilitating its invasion from southern to northern lakes. The northwest limit of the Alps, where Lakes Geneva, Bourget and Annecy are located was not considered by Keller et al. (2008). Similar patterns than in northern lakes could, however, be expected.

The establishment of *D. galeata* and subsequent changes in the reproductive strategies are, however, closely related to trophic status and the magnitude of eutrophication of lakes (Brede et al. 2009, Rellstab et al. 2011). For instance, in Lake Brienz, which has a trophic status as well as a eutrophication history (maximum [TP] was $\approx 20 \mu\text{gP L}^{-1}$) similar to Lake Annecy, no *D. galeata* ephippia has been found (Rellstab et al. 2011). In contrast, in Lakes Constance which underwent a more intense eutrophication (maximum [TP] was $87 \mu\text{gP L}^{-1}$) as Lakes Geneva and Bourget, *D. galeata* ephippia were found (Brede et al. 2009). The lack of *D. galeata* ephippia in the egg bank of Lake Annecy supports the hypothesis that *D. galeata* can not establish in very oligotrophic lakes as was shown by Rellstab et al. (2011) in Lake Brienz. On the other hand, the presence of resting eggs with *D. galeata* genotype from sediment layers before eutrophication in Lakes Geneva and Bourget indicates that *D. galeata* was present before eutrophication but its effects in disrupting reproductive strategies in *Daphnia* communities increased during eutrophication.

IV.5.3. Past changes in the reproductive behaviour in *D. longispina* species complex

The paleogenetic analyses showed long-term changes in the reproductive strategies of *Daphnia* as indicated by disappearance of sexual reproduction in some parental species in Lake Annecy. Indeed, while L1 performed sexual reproduction all over the time period, L2 did not trigger sexual reproduction during the maximum of eutrophication (oligo-mesotrophic status, Perga et al. 2010) suggesting that L1 and L2 present either different triggers for sexual reproduction or different sensitivity of their triggers. We propose rather the second hypothesis because during the eutrophication and re-oligotrophication periods, the impacts of fish predation pressure (i.e., strong) and climate warming (i.e., none) were similar between them, while nutrient level changed (Perga et al. 2010, Alric et al. submitted). Therefore, the sexual reproduction of L2 seems to be directly triggered by the lake trophic status in particular the low food conditions.

On the other hand, the occurrence and increase of hybridization events were detected in Lakes Geneva and Bourget during the eutrophication period. Hybridization events required temporal and spatial co-occurrence of males and females of two species. In *Daphnia cucullata-galeata-longispina* species complex, there is a species-specific timing of sexual reproduction (Wolf 1987, Spaak 1996, Jankowski and Straile 2004). In contrast, an analysis of spatial patterns within *Daphnia cucullata-galeata-longispina* species complex in Lake Plußsee did not detect a taxon specific spatial distribution of sexual stages (Spaak et al. 2004). Therefore, hybridization events in Lakes Geneva and Bourget imply that eutrophication has decreased pre-mating barriers (i.e., temporal occurrence of sexual stages) between *D. galeata* and *D. longispina*. These results are consistent with hybridization events recorded in Lakes Constance and Greifensee following eutrophication (Brede et al. 2009). However, although there is increasingly evidence for a relationship between environmental forcings and hybridization events, very few is known about the processes responsible for such patterns, i.e. the forcings which trigger simultaneous sexual reproduction of two syntopic *Daphnia* species. Hybridization may arise from the response of *Daphnia* species to the same trigger or to different triggers which synchronize when the lake shift to a higher trophic state. Among previously identified triggers for sexual reproduction, crowding and fish predation pressure might be those which affect timing when lake trophic status changes.

An experimental study in mesocosms showed that increased nutrient concentrations resulting in crowding triggered a simultaneous induction of sexual reproduction by *D. galeata* and *D. longispina* (Jankowski 2002). In addition, in Lake Constance, *D. galeata* exhibited a greater dependence on sexual reproduction in the presence of zooplanktivorous fish than *D. longispina* (Jankowski and Straile 2004). According to the paleolimnological reconstruction based on cladoceran carapace remains, the abundance of cladocerans as well as intensity of top-down control by planktivorous fish were shown to increase with the higher nutrient concentrations in Lakes Geneva and Bourget (Alric et al. submitted). Therefore, we can suppose that in eutrophied Lakes Geneva and Bourget, crowding was a trigger of simultaneous sexual activity by *D. galeata* and *D. longispina*. Fish predation pressure could also disrupt the timing of sexual reproduction of *D. galeata* increasing the probability of encounter with sexual stages of *D. longispina*.

Surprisingly, during the re-oligotrophication period, hybridization events were, in contrast to Lake Geneva, still recorded in Lake Bourget highlighting that trophic status would not be the only forcing driving reproductive strategies and subsequent hybridization. A stronger fish predation pressure in Lake Bourget cannot explain this discrepancy in hybridization events since a previous study showed that fish predation pressure decreased during the re-oligotrophication period in this lake (Alric et al. submitted). This study also showed that cladoceran community in Lake Bourget was the most sensitive, as compared Lakes Annecy and Geneva, to climate warming. The effect of increased air temperature could disrupt reproductive strategies through alterations of the composition of primary producers and subsequent changes in the competition between *D. galeata* and *D. longispina*. For instance, climate warming is suspected to promote summer bloom of filamentous cyanobacteria (Paerl and Huisman 2009) and such blooms of the filamentous cyanobacteria *Planktothrix rubescens* have been observed in Lake Bourget (but not Geneva) from the 1990s (Jacquet et al. 2005). Periods of blooms may be considered as a nutritional stress for filter-feeders such as *Daphnia* since filamentous cyanobacteria are a poor quality food due to their potential toxicity, low nutritional content and the disadvantageous interference of their morphology with food-collection mechanisms of *Daphnia* (Gliwicz and Siedlar 1980, Hawkins and Lampert 1989). Under such conditions, *D. longispina* may be favoured over *D. galeata* as the result of a better adjustment of their filtering apparatus (Stich and Lampert 1984).

Climate warming could be considered as a trigger of sexual activity of *D. galeata* decreasing the temporal pre-zygotic barriers with *D. longispina*, thereby increasing the probability of encounter between sexual stages.

IV.5.4. Potential processes at the origin of the directionality of hybridization

One potential consequence of interspecific hybridization is introgression (i.e., the spread of genetic material of one species into the gene pool of the other) which is closely related to directionality of hybridization. In Lakes Geneva and Bourget, the combination of microsatellite and mitochondrial data showed bidirectionality in interspecific hybridization. The reproductive behaviour of males may influence the directionality of interspecific hybridization. In contrast to calanoid copepods (Katona 1973) or cladocera *Moina brachiata* (Forró 1997), the mate detection abilities of male *Daphnia* are considerably less well-developed (Brewer 1998, Winsor and Innes 2002). A microcosm experiment over the behavioural interaction between male and female *Daphnia pulicaria* showed that males did not discriminate in their choice of mate (i.e. male or female) until contact suggesting a poorly developed chemoreceptive system (Brewer 1998). The prevalence of interspecific hybridization within the *Daphnia cucullata-galeata-longispina* species complex (Schwenk and Spaak 1995) suggests thus that the chemoreceptive system that identifies sexual females is of low specificity in *Daphnia* males, at least, to for given species complex (Winsor and Innes 2002). This phenomenon may be expanded by the timing occurrence between male and female of *Daphnia* taxa. Indeed, an early investment in males has already been observed in lakes (e.g., Lynch 1983, Spaak 1995): since males need several days after being released from the brood chamber to mature (Yamplosky 1992), early male production has been regarded as a strategy to optimize the timing of mating when conditions become unfavorable and as soon as females switch to sexual reproduction (Zaffagnini 1987). Hybridization may then occur when the induction of sexual females by one *Daphnia* species is interposed between the production of males and females by another *Daphnia* species where the reproductive behaviour of males could increase the probability of encounter between sexual stages of *D. galeata* and *D. longispina*. In addition, unbalanced production of sexual stages among syntopic species may also drive the directionality of interspecific hybridization.

Several laboratory studies have reported induction of males without subsequent production of sexual eggs (e.g., Ferrari and Hebert 1982, Hobaek and Larsson 1990). One potential explanation may be the varying energy demands between males and sexual eggs production. The production of males seems to be energetically similar to asexual propagation, because males and parthenogenetic progeny can be produced in the same clutch (Olmstead and Leblanc 2002). In contrast, it is estimated in *Daphnia pulex* that the production of one ephippium (i.e., two sexual eggs), is energetically equivalent to the production of nine males (Lynch 1983). We can suppose that *D. galeata* and *D. longispina* differ in their sexual stages production as in Lake Constance where, *D. galeata* can produce up to 33 times more sexual females than *D. longispina* (Jankowski 2002). Therefore, when environmental perturbations trigger the simultaneous induction of sexual stages in two syntopic *Daphnia* species, the reproductive behaviour of males, timing of the occurrence of males and sexual females and unbalanced sexual stages production among syntopic species can result in directionality of the hybridization process. This hypothesis was supported by our results since, in both lakes, a higher level of mitochondrial introgression from *D. galeata* than *D. longispina* was observed. A previous study on the directionality of hybridization among North American *Daphnia* species showed also a bidirectional asymmetric hybridization (Taylor and Hebert 1993). They explained this asymmetry in the contribution of species to maternal genome by postulating that females of the common species and males of the rare species would form interspecific hybrids. In addition, our data on present pelagic *Daphnia* population in Lake Geneva showed that on average *D. galeata* was the most abundant species in the asexual and sexual population. Therefore, we can assume that the bidirectional hybridization in Lakes Geneva and Bourget could follow the model of bidirectional asymmetric hybridization by Taylor and Hebert (1993) (see above). These results may seem surprising since the hypothesis of unidirectional introgression was previously proposed for *Daphnia cucullata-galeata-longispina* species complex (Schwenk 1993).

To conclude, the long-term changes in environmental conditions induced changes in reproductive strategies of *Daphnia* populations. Depending on time periods, it seems that changes in reproductive strategies were driven by different combinations of forcings. Similarities in the drivers of the structure of cladoceran communities (Alric et al. submitted) and reproductive strategies may be emitted, in particular TP which was the main driver of both processes during the eutrophication period.

In addition, in Lake Bourget during the re-oligotrophication period, climate warming may interfere with both the structure of cladoceran communities and *Daphnia* reproductive strategies. In contrast, in Lake Geneva, the recovery of reproductive strategy of *Daphnia* suggests that fish predation pressure does not affect this process, in contrast to what has been evidenced on the structure of cladoceran communities. The observation of hybridization events during the eutrophication and re-oligotrophic period implies a disturbance in the timing of sexual reproduction with an overlap in the induction of sexual stages by the two parental taxa. We can assume that the complexity of the impact of eutrophication and climate warming through trophic interactions can be the triggers of this process. Therefore, this study raises the question of a more thorough investigation of triggers inducing the simultaneous production of sexual stages by two syntopic species in a context of multiple perturbations, environmental conditions that will be increasingly common in the future.

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IV.6. Appendix A: Data set of *D. galeata* and *D. hyalina* laboratory clones originating from 19 European lakes.

Table IV.1. List of 39 reference clones, including their genetic identification by different marker systems and sampling location.

Code	Allozyme-type	Microsatellites	Lake	Country
AROS_5	Gal	Gal	Arosa Obersee	Switzerland
AROS_8	Gal	Gal	Arosa Obersee	Switzerland
BODO_807	Gal	Gal	Bodensee	Germany
BODO_809	Gal	Gal	Bodensee	Germany
COMA_270	Gal	Gal	Lago di Comabbio	Italy
COMA_265	Gal	Gal	Lago di Comabbio	Italy
ENDI_44	Gal	Gal	Lago d'Endine	Italy
ENDI_45	Gal	Gal	Lago d'Endine	Italy
ENDI_56	Gal	Gal	Lago d'Endine	Italy
G100	Gal	Gal	Tjeukemer	Netherlands
GREI_805	Gal	Gal	Greifensee	Switzerland
GREI_814	Gal	Gal	Greifensee	Switzerland
ISEO_80	Gal	Gal	Lago d'Iseo	Italy
ISEO_86	Gal	Gal	Lago d'Iseo	Italy
MURT_8	Gal	Gal	Murtensee	Switzerland
PFAF_826	Gal	Gal	Pfäffikersee	Switzerland
PFAF_833	Gal	Gal	Pfäffikersee	Switzerland
SEGR_196	Gal	Gal	Lago di Segrino	Italy
VARE_249	Gal	Gal	Lago di Varese	Italy
VARE_250	Gal	Gal	Lago di Varese	Italy
VARE_259	Gal	Gal	Lago di Varese	Italy
ZH_U_802	Gal	Gal	Zürichsee	Switzerland
ZUGE_821	Gal	Gal	Zugersee	Switzerland
ZUGE_829	Gal	Gal	Zugersee	Switzerland
BODO_815	Lon	Lon	Bodensee	Germany
BODO_818	Lon	Lon	Bodensee	Germany
COMO_146	Lon	Lon	Lago di Como	Italy
COMO_157	Lon	Lon	Lago di Como	Italy
H7	Lon	Lon	Bodensee	Germany

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MAGG_229	Lon	Lon	Lago Maggiore	Italy
MAGG_230	Lon	Lon	Lago Maggiore	Italy
MONA_296	Lon	Lon	Lago di Monate	Italy
MONA_398	Lon	Lon	Lago di Monate	Italy
NEUE_802	Lon	Lon	Neuenburgersee	Switzerland
NEUE_803	Lon	Lon	Neuenburgersee	Switzerland
SARN_804	Lon	Lon	Sarnersee	Switzerland
SARN_805	Lon	Lon	Sarnersee	Switzerland
WALE_804	Lon	Lon	Walensee	Switzerland
WALE_806	Lon	Lon	Walensee	Switzerland

Gal, Lon are the abbreviations for *D. galeata* and *D. longispina*, respectively.

V. Synthèse générale et perspectives

V.1. Les assemblages fossiles de cladocères et leur représentativité dans les grands lacs profonds

Le premier objectif de cette thèse vise à évaluer la représentativité des restes parthénogénétiques (i.e., exosquelettes) et issus de la reproduction sexuée (i.e., éphippies) vis-à-vis des communautés sources de cladocères. Cette étape est nécessaire afin d'estimer la pertinence de notre modèle biologique pour les reconstructions paléolimnologiques dans les grands lacs profonds.

Nos résultats montrent que les niveaux de représentativité des assemblages fossiles varient entre les types de restes et entre les taxons. L'intégration des changements de la structure en taille des communautés sources de cladocères par les assemblages fossiles d'exosquelettes présente également certaines limites.

- (i) La composition taxonomique des restes parthénogénétiques produits par les cladocères et collectés dans les trappes à sédiments du lac d'Aiguebelette reflètent relativement bien celles de la colonne d'eau, pour les espèces dominantes (i.e., *Daphnia sp.*, *Eubosmina spp* et *Diaphanosoma brachyurum*) (Chapitre II). A l'inverse, la composition taxonomique des éphippies des Daphnies au cours d'un cycle annuel dans le lac Léman ne concorde pas avec la composition taxonomique des individus de la colonne d'eau (Chapitre IV).
- (ii) Les changements saisonniers dans la taille moyenne des restes parthénogénétiques récupérés dans les trappes reflètent ceux des taxons dominants. On observe cependant une sous-estimation systématique des tailles estimées à partir de ces restes parthénogénétiques sur l'ensemble de la période d'étude (Chapitre II).
- (iii) Les restes d'exosquelettes des espèces littorales sont sporadiquement représentés dans les trappes, comme le résultat de l'influence de la morphométrie du lac sur la remobilisation et le transport des sédiments littoraux vers les zones profondes (Chapitre II).

- (iv) La représentativité des assemblages de restes parthénogénétiques semble dépendre de l'approche méthodologique, et en particulier, de la maille du tamis utilisé pour extraire les restes des sédiments (Chapitre II).

Table V.1. Etudes utilisant les restes parthénogénétiques et/ou les éphippies pour reconstruire l'impact de perturbations environnementales similaires.

Lacs	Z _{moy} ^a	Type de reste	Question	Référence
Paul	3.9	Parthénogénétique	Prédation	1
Peter	6.0			
Paul	3.9	Parthénogénétique	Prédation	2
Peter	6.0			
Tuesday	6.9			
30 lacs danois	3.7	Parthénogénétique + éphippie	Prédation	3
Avalanche	19.8	Parthénogénétique + éphippie	Prédation et abondance des Daphnies	4
Kräkenes	14.0	Parthénogénétique + éphippie	Reconstruction de la température	5
30 lacs danois	3.7	Ephippie	Prédation	6
Apoka	1.6	Parthénogénétique	Statut trophique	7
Fuxian	89.7	Parthénogénétique	Prédation et statut trophique	8
Biwa	41.2	Ephippie	Réchauffement climatique	9
Vesijärvi	6.8	Parthénogénétique + éphippie	Prédation et statut trophique	10
6 lacs d'Alaska	37.0	Parthénogénétique	Prédation et nutriments	11

^a Z_{moy}: profondeur moyenne du lac(en m)

1. Kitchell et Kitchell (1980), 2. Sanford (1993), 3. Jeppesen et al. (1996), 4. Verschuren et Marnell (1997), 5. Duigan et Birks (2000), 6. Jeppesen et al. (2002), 7. Shumate et al. (2002), 8. Liu et al. (2009), 9. Tsugeki et al. (2009), 10. Nykänen et al. (2010), 11. Chen et al. (2011).

Une telle fidélité dans la représentation des communautés sources par les restes parthénogénétiques est en partie liée à la morphométrie des lacs profonds qui permet un processus de sédimentation continu dans le temps tout en minimisant les potentielles perturbations de ce processus (e.g., remobilisation, resuspension des sédiments, transport littoral) (Chapitre II). Nos résultats soulignent toutefois un manque de représentativité des espèces rares (telles que *Bosmina longirostris*) et une sous-estimation de la taille moyenne corporelle des individus par les restes parthénogénétiques. Ces limites pourraient éventuellement affecter les interprétations des reconstructions paléolimnologiques des lacs. Pour les espèces dites rares, nous proposons dans le Chapitre II de les considérer en terme de présence/absence dans les reconstructions des trajectoires écologiques des communautés de cladocères. Un tel traitement de *B. longirostris* ou d'autres espèces plus littorales (e.g., *chydorus* sp.) peut néanmoins apporter des informations fonctionnelles sur le contrôle "top-down" et sur l'état trophique du lac (Ravera et Praise 1978, Perga et al. 2010). Dans les sédiments des lacs Léman, du Bourget et d'Annecy, les contributions relatives moyennes de *Bosmina longirostris*, *Sida crystallina* et *chydorus* sp. (espèces plus littorales) ainsi que *Bythotrephes longimanus* et *Leptodora kindtii* (des cladocères prédateurs) peuvent respectivement aller jusqu'à 18%, 14%, 8%, 2% et 4% de la communauté totale. Ce niveau de contribution permet d'inclure ces taxons en tant que tels dans notre analyse statistique (modèle additif généralisé, GAM) (Hastie et Tibshirani 1990) et pas seulement de les considérer en terme de présence/absence (Chapitre III). En ce qui concerne la sous-estimation de la taille corporelle des cladocères, nous pouvons nous affranchir d'un tel biais puisque celle-ci est observée sur l'ensemble de la période d'étude et l'information pertinente concerne ses variations relatives au cours du temps (Chapitre II).

Nos résultats mettent également en évidence que selon le type de restes considérés (i.e., parthénogénétique ou issus de la reproduction sexuée), les assemblages fossiles de cladocères archivés dans les sédiments de nos lacs d'étude (des grands lacs profonds) reflètent une image plus ou moins cohérente des communautés sources. Dans les reconstructions paléolimnologiques cependant, les restes parthénogénétiques et les éphippies sont souvent utilisés séparément ou en combinaison pour aborder des questions similaires (Table V.1). Par exemple, dans le lac Vesijärvi, l'impact de l'introduction de poissons et de la réduction des charges externes en phosphore sur les communautés de cladocères est estimé au travers des restes parthénogénétiques de *B. longirostris* et des éphippies de *Daphnia* sp. (Nykänen et al. 2010).

Ceci laisse penser que ces deux types de restes peuvent être utilisés de façon interchangeable, en fonction de leur facilité d'extraction et d'analyse dans un contexte donné. Cependant, d'après nos résultats, dans les grands lacs profonds, ces deux types de restes ne peuvent pas être utilisés indifféremment et le choix du type de restes est crucial selon la question posée. En effet, l'image relativement fidèle des communautés sources de cladocères fournie par les restes parthénogénétiques, tant sur leurs caractéristiques compositionnelles que structurelles en fait le type de restes le plus pertinent pour répondre à l'objectif premier de cette thèse, c'est-à-dire reconstruire la trajectoire écologique des communautés de cladocères pélagiques des lacs Léman, du Bourget et d'Annecy et évaluer l'impact des trois perturbations considérées sur les réseaux trophiques pélagiques énoncées dans le Chapitre I. Plus précisément, les modifications des contrôles "bottom-up" et "top-down" issus des perturbations locales et régionales peuvent être intégrées dans les assemblages fossiles de cladocères respectivement au travers de l'enregistrement des changements dans les abondances et dans la structure en taille des restes parthénogénétiques de cladocères.

Les éphippies sont couramment utilisées dans des lacs peu profonds et les mares temporaires pour reconstruire les changements dans la composition des communautés sources (au travers de leurs caractéristiques morphologiques ou génétiques, Yan et al. 1996, Mergeay et al. 2004, Mergeay et al. 2006) ainsi que dans la pression de prédation par les poissons (au travers de leur taille, Jeppesen et al. 2002, Nykänen et al. 2006). La pertinence de telles approches semble toutefois limitée dans nos grands lacs profonds, puisque les banques d'éphippies archivées dans les sédiments procurent une image sélective des individus qui ont opéré une reproduction sexuée, et ne renseignent donc ni sur la composition taxonomique des populations de la colonne d'eau, ni même sur leur structure en taille (résultats personnels). Les divergences observées entre le niveau de représentativité des éphippies dans nos grands lacs profonds par rapport aux lacs peu profonds et les mares temporaires peuvent venir d'une reproduction sexuée plus épisodique dans les lacs grands profonds (Hebert 1978). Nous avons donc choisi d'étudier l'architecture génétique des banques d'éphippies selon un objectif plus évolutif, c'est-à-dire de reconstruire les changements dans le comportement de reproduction des populations de *Daphnies* en réponse aux trois perturbations considérées.

Une perspective ultérieure consiste à aborder ces résultats sous des aspects tenant aux processus de spéciation, au travers notamment de l'estimation des distances génétiques entre les différentes espèces de Daphnies d'un même système, qui peut nous informer sur leur potentiel de reproduction sexuée interspécifique.

V.2. Les trajectoires écologiques des lacs et leur vulnérabilité face aux changements climatiques

V.2.1. Les limites de l'estimation des trois perturbations environnementales

L'approche paléolimnologique présente l'avantage, sur les méthodes d'écologie plus classiques, de donner accès à de longues échelles de temps. Cependant, le désavantage d'une telle approche est que l'interprétation des reconstructions environnementales est basée essentiellement sur des estimateurs indirects des communautés biologiques et des paramètres environnementaux. Par exemple, la très faible quantité de restes de poissons archivés dans les sédiments lacustres rend difficile l'estimation directe des populations pisciaires (Patterson et Smith 2001, Davidson et al. 2003) et par conséquent la reconstruction des changements dans l'intensité de planctivorie. Une estimation indirecte peut être réalisée au travers de l'utilisation de différents types de restes de cladocères (Jeppesen et al. 2001). Notre choix s'est porté sur la taille des griffes postabdominales de Daphnies comme estimateur des changements dans l'intensité de la planctivorie des poissons d'après les résultats précédemment discutés. En effet, la réponse des cladocères à une augmentation de la pression de prédation par les poissons s'illustre par une maturité plus rapide, une plus petite taille au stade adulte et une plus forte fécondité (e.g., Gliwicz et al. 1981, Post et McQueen 1987, Macháček 1991, Stibor 1992, Boersma et al. 1999). Les changements en taille à l'échelle de la communauté et de l'individu chez les cladocères sont cependant fonction d'interactions complexes entre la pression de prédation et d'autres facteurs environnementaux, notamment la qualité et la quantité de nourriture ainsi que le climat (Figure V.1). L'impact des modifications dans le niveau trophique lacustre est relativement complexe. Par exemple, la taille corporelle des cladocères peut augmenter avec la quantité de nutriments comme le résultat d'un déclin de la limitation dans la ressource alimentaire (e.g., Neill 1981, Foran 1986, Lynch 1989, Boersma et Vijverberg 1995).

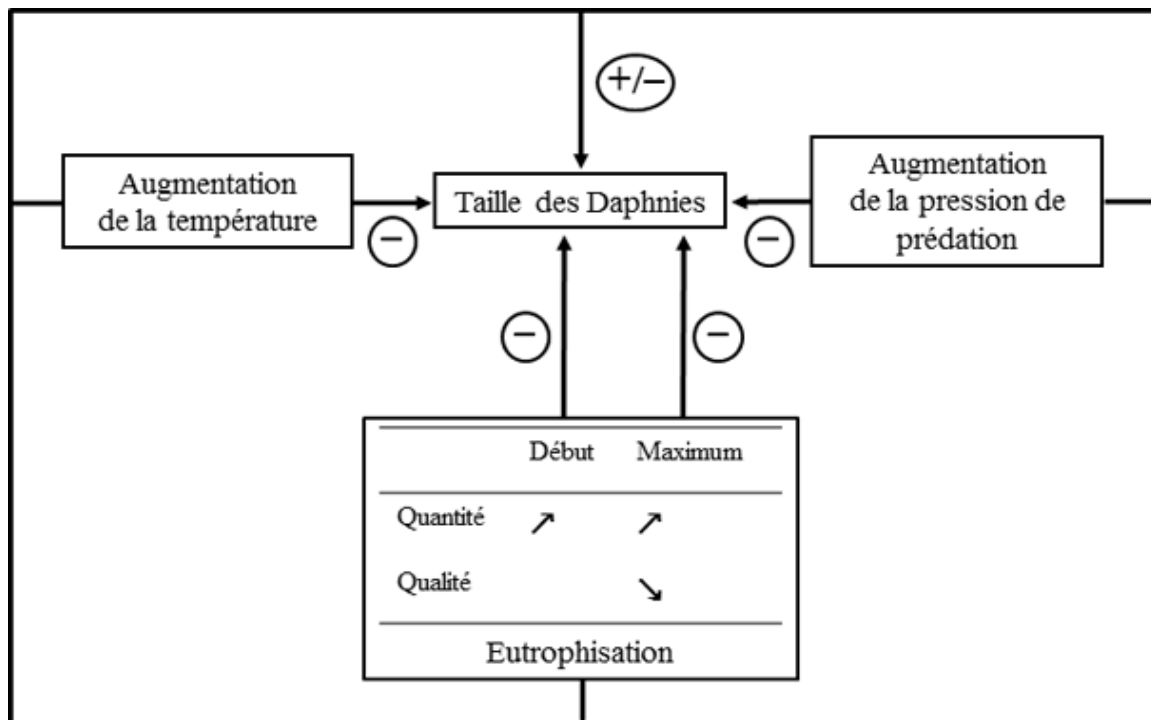


Figure V.1. Représentation schématique de l'influence du réchauffement climatique et des changements dans le niveau en nutriments et dans la pression de prédation par les poissons planctonophages sur la taille corporelle des cladocères pélagiques.

A partir d'un certain niveau trophique cependant, la qualité nutritionnelle des communautés phytoplanctoniques pour les herbivores diminue, entraînant ainsi une diminution de la taille corporelle des cladocères (e.g., Webster et Peters 1978, Gliwicz et Lampert 1990, DeMott et al. 2001). Dans les trois lacs, la taille des Daphnies commence à diminuer dès le début de l'eutrophisation, tandis que la tendance inverse devrait être observée si l'augmentation dans la quantité en ressource était le forçage direct contrôlant la taille des Daphnies. De même, l'augmentation de la température liée au changement climatique n'exerce un effet significatif qu'à partir de la fin des années 1980 (Chapitre III), excluant de fait la température comme facteur de forçage important sur la taille des cladocères sur la majorité de la période d'étude. Par contre, les changements temporels de taille des Daphnies sont inversement corrélés avec les captures de pêches dans les lacs Léman, du Bourget et d'Annecy (Figure V.2), confortant ainsi l'hypothèse que la taille des Daphnies est essentiellement contrôlée par la pression de prédation dans les lacs d'étude.

Trois estimateurs différents ont été utilisés (Chapitre III) pour reconstruire les changements dans les concentrations de la colonne d'eau en phosphore. L'estimateur pour le lac Léman est celui qui pose le moins de problème puisqu'il s'agit des concentrations en phosphore mesurées dans la colonne d'eau dans le cadre du suivi de la qualité des eaux du lac (géré par la Commission Internationale pour la Protection des Eaux du Léman et l'INRA). Par contre, dans les deux autres lacs, des différences entre les concentrations en phosphore mesurées dans la colonne d'eau et les reconstructions à partir des estimateurs peuvent être dégagées. Par exemple, dans le lac du Bourget, le déclin des concentrations en phosphore (reconstruite à partir de l'estimateur) commence en 1976 alors que selon le suivi dans la colonne d'eau, le déclin commence en 1983. Pour le lac d'Annecy, une différence dans l'estimation des concentrations en phosphore entre le suivi et les reconstructions est visible durant les années 1990. Par conséquent, l'utilisation de trois estimateurs différents des changements dans les concentrations en phosphore ne pourrait-elle pas influencer les résultats des GAM ? Pour vérifier cela, il serait intéressant de tester si les deux estimateurs utilisés dans les lacs du Bourget et d'Annecy génèrent des estimations équivalentes des changements passés dans les concentrations en phosphore.

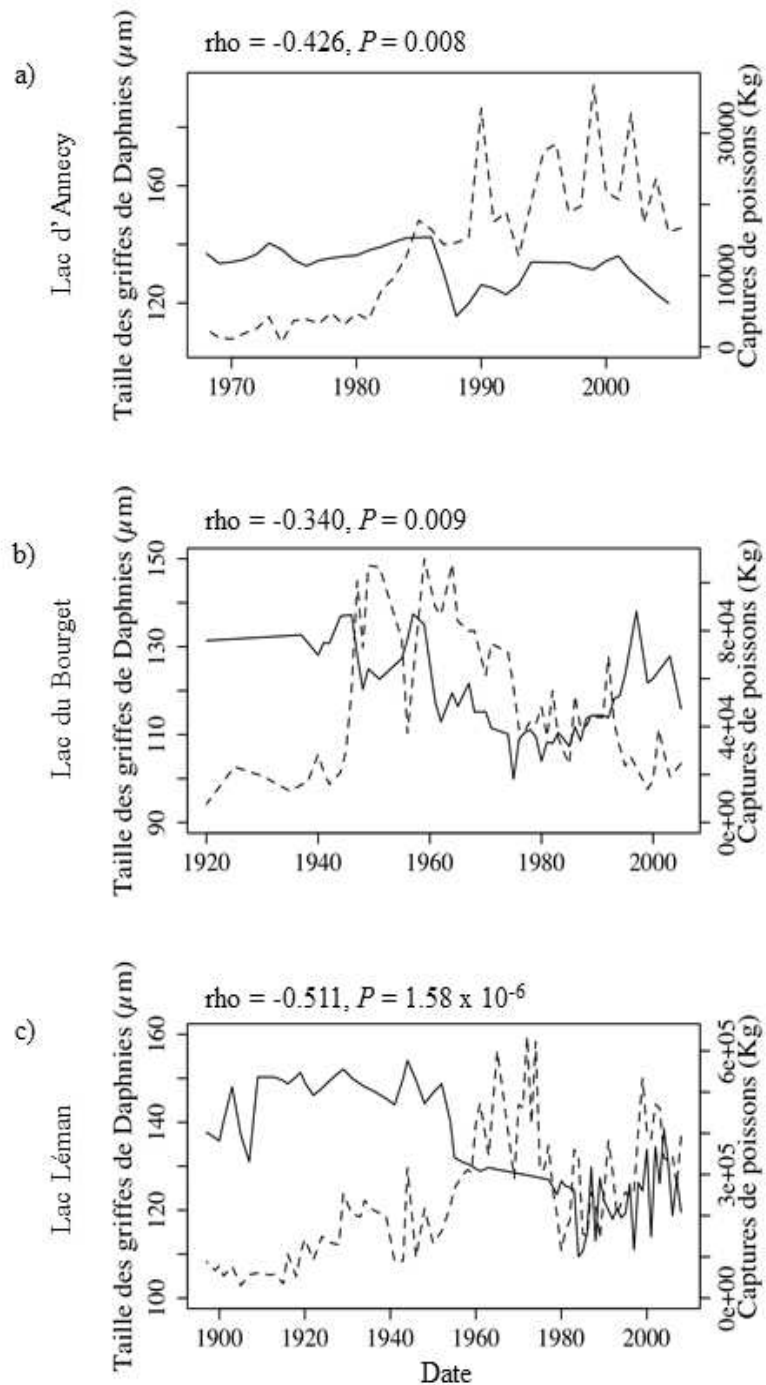


Figure V.2. Relation entre la taille des griffes postabdominales de Daphnies et les captures de pêches dans (a) le lac d'Annecy, (b) le lac du Bourget et (c) le lac Léman. Les captures de poissons correspondent respectivement à différents types de poissons entre les trois lacs : (a) Corégone, (b) et (c) Corégone + Perche + Gardon.

La solution la plus simple serait cependant, d'utiliser le même estimateur pour les trois lacs, mais pour le moment cela n'est pas possible puisque nous n'avons pas les données nécessaires. Dans cette optique deux solutions s'offrent à nous :

- (i) reconstruire les changements dans les concentrations en phosphore à partir d'une fonction de transfert basée sur les diatomées comme pour le lac du Bourget (cf., Chapitre III). Un tel travail est actuellement en cours sur les lacs Léman et d'Annecy et est effectué par Vincent Berthon dans le cadre de sa thèse.
- (ii) utiliser un autre estimateur telle que la composition en isotope stable de l'azote de la matière organique sédimentaire qui retrace de façon relativement fiable l'histoire de l'eutrophisation dans le lac d'Annecy (Perga et al. 2010). De telles données sont actuellement en cours d'acquisition.

Enfin, nous n'avons considéré comme composante climatique, que les changements de la température de l'air alors que le climat inclut aussi des paramètres de précipitations et de rayonnements solaires (Leavitt et al. 2009). Le rôle du climat dans la trajectoire des communautés de cladocères n'est donc que partiellement abordé dans cette étude. Cependant, et contrairement aux lacs boréaux peu profonds (Wissel et al. 2011), l'altération de la stratification thermique de la colonne d'eau en raison du réchauffement de la température de l'air (Edinger et al. 1968) est l'une des principales voies d'actions du climat dans les grands lacs profonds tempérés (e.g., Straile et al. 2003, Molinero et al. 2006, Obertegger et al. 2007). De plus, aucun changement significatif dans les précipitations n'a été détecté pour l'instant (Chapitre III). Enfin, nous ne disposons pas de jeux de données suffisamment longs sur le rayonnement solaire (entre 10 et 30 ans) pour être en mesure de tirer des conclusions sur l'impact potentiel de cette voie d'action du climat sur les lacs.

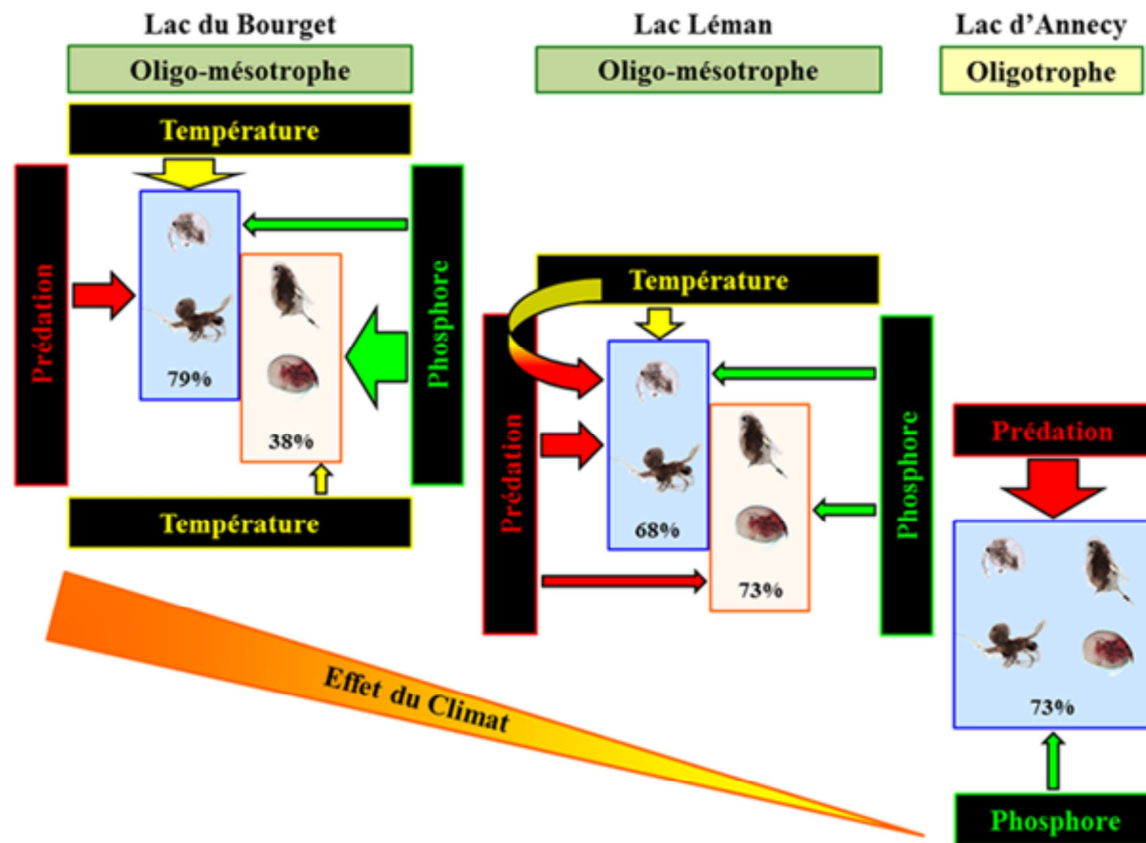


Figure V.3. Schéma récapitulatif de l'impact des trois perturbations environnementales sur les communautés de cladocères pélagiques des lacs du Bourget, Léman et d'Annecy. Pour les lacs du Bourget et Léman, le carré bleu regroupe les Bosmines et les cladocères prédateurs, et le carré orange regroupe les Daphnies et les espèces littorales selon les composantes principales de l'ACP réalisée sur les abondances des restes dans les carottes sédimentaires. Pour le lac d'Annecy, les Bosmines, les Daphnies, les cladocères prédateurs et littoraux sont regroupés sur la même composante. L'épaisseur des flèches correspond à l'intensité de la contribution de chaque perturbations environnementales dans la variance des communautés de cladocères selon les résultats des GAM, et les pourcentage dans chaque carrée correspond à la variance expliquée par les GAM (voir Chapitre III pour plus de détails.).

V.2.2. La réponse des communautés de cladocères au travers de deux caractéristiques structurantes

La dynamique des populations (en terme d'abondance) et les comportements de reproduction des communautés de cladocères sont étroitement liés mais également fortement influencés par les conditions environnementales. Ici, l'influence des perturbations locales et régionales sur les comportements de reproduction est estimée principalement au travers de l'apparition d'événements d'hybridation interspécifique dans le complexe d'espèce *Daphnia cucullata-galeata-longispina*. Dans les lacs d'étude, de profondes modifications des dynamiques des populations et des comportements de reproduction dans les communautés de cladocères sont observées comme le résultat d'interactions complexes entre le réchauffement climatique et les deux perturbations locales.

- (i) Avant les années 1980 (correspondant à la période d'eutrophisation des lacs), le phosphore est identifié comme le principal forçage de la trajectoire des communautés de cladocères (Chapitre III) ainsi que de l'apparition d'événements d'hybridation interspécifique chez les Daphnies (Chapitre IV).
- (ii) A partir des années 1980 (correspondant à la période de ré-oligotrophisation des lacs), le phosphore ne semble plus être le forçage principal de ces deux caractéristiques des communautés de cladocères. L'utilisation de GAM montre que les trajectoires des communautés de cladocères sont contrôlées par des interactions entre les différentes perturbations (Chapitre III) (Figure V.3). Une différence dans l'apparition d'événement d'hybridation interspécifique entre le lac Léman (absence d'hybridation) et le lac du Bourget (enregistrement d'hybridation) est aussi observée (Chapitre IV).

Globalement, ces résultats montrent que la dynamique des populations et le comportement de reproduction des Daphnies sont influencés par l'ensemble des perturbations locales et régionales (Chapitre III, IV). Les communautés de cladocères répondent, cependant, aux perturbations avec des sensibilités différentes entre les lacs d'étude. De même, la sensibilité des comportements de reproduction des Daphnies à ces perturbations diffère entre les espèces.

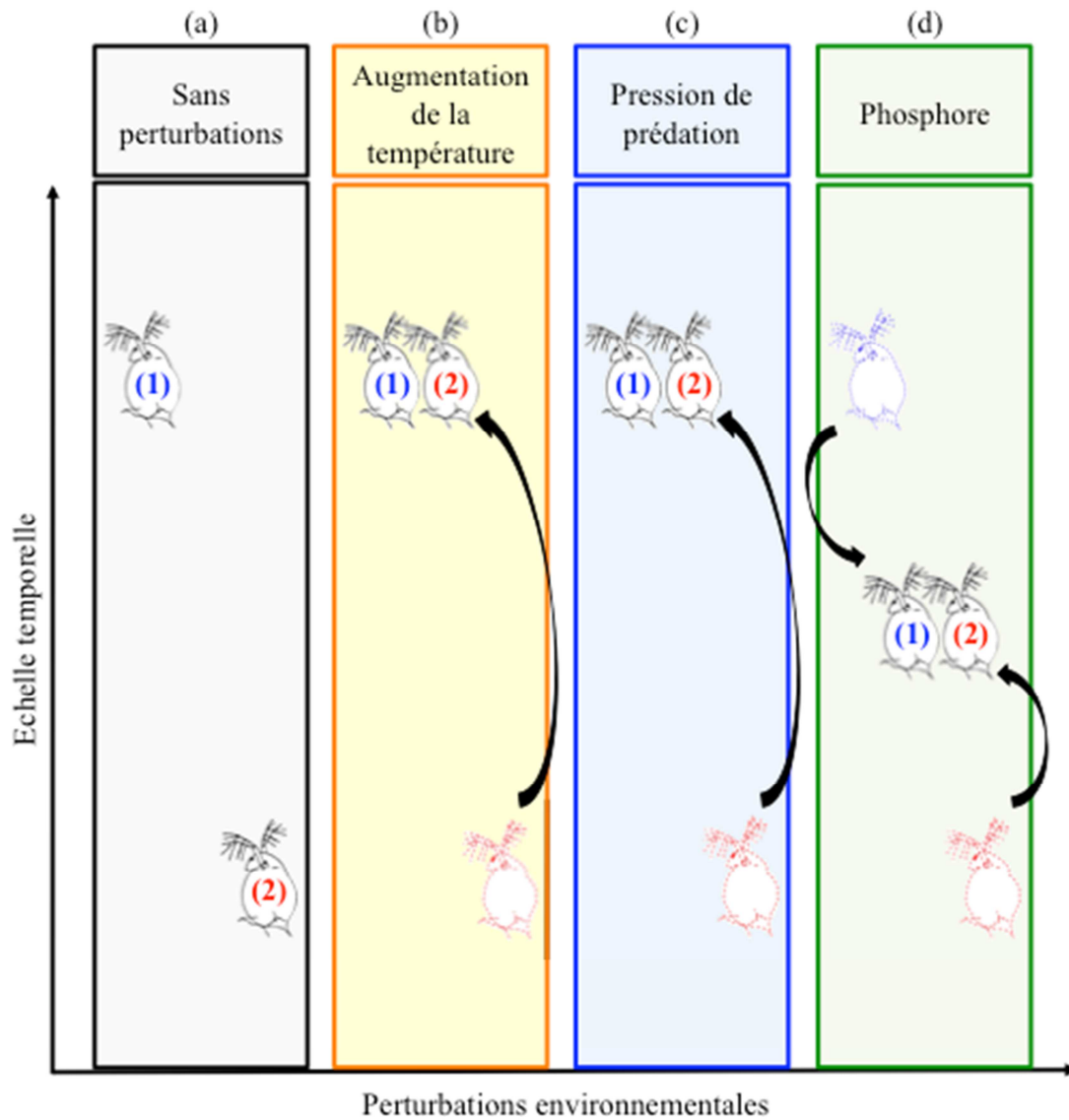


Figure V.4. Modèle conceptuel illustrant l'influence respective des trois forçages environnementaux (augmentation de la température et changement dans le niveau en phosphore et dans la pression de prédation par les poissons zooplanctivores) sur l'apparition d'hybridation interspécifique entre *D. longispina* (1) et *D. galeata* (2). L'axe y correspond à la période de temps à laquelle les deux espèces de Daphnies basculent vers une reproduction sexuée. *D. galeata* et *D. longispina* présentent des périodes de reproduction sexuée distinctes dans le temps (a). Les trois forçages environnementaux peuvent modifier la période de temps de reproduction sexuée des deux espèces entraînant un chevauchement temporel entre les deux espèces résultant dans des évènements d'hybridation interspécifique (b), (c) et (d).

Durant la période de ré-oligotrophisation, la réponse de la dynamique des populations des communautés de cladocères au réchauffement climatique est différente entre les lacs comme le résultat d'une régulation de l'intensité de son impact par les perturbations locales (Chapitre III) (Figure V.3). La sensibilité au réchauffement climatique semble être liée au statut trophique des lacs. En effet, les communautés de cladocères des lacs Léman et du Bourget, plus eutrophes que le lac d'Annecy, présentent les plus fortes réponses au réchauffement climatique. Le statut trophique des lacs n'est pas, cependant, le seul forçage local à moduler l'influence du réchauffement climatique. En effet, les lacs Léman et du Bourget présentent des statuts trophiques similaires mais l'impact du réchauffement climatique semble s'opérer selon différentes voies d'actions (Figure V.3). Dans les deux lacs, le réchauffement climatique affecte les communautés de cladocères directement au travers des processus physiologiques. Dans le lac du Bourget, l'altération de la composition de la communauté phytoplanctonique en réponse à l'augmentation de la température influence les communautés de cladocères. Dans le lac Léman, un impact indirect du réchauffement climatique affecte également les communautés de cladocères mais sous la forme d'un couplage avec la pression de prédation par les poissons, montrant que ce forçage local peut également influencer la sensibilité des communautés de cladocères au réchauffement climatique.

L'étude de l'architecture génétique des banques d'éphippies de *Daphnies* archivées dans les sédiments des lacs Léman, du Bourget et d'Annecy montrent que les comportements de reproduction des deux espèces parents identifiées dans les lacs d'étude (i.e., *D. galeata* et *D. longispina*) sont différemment influencés par les trois perturbations considérées (Chapitre IV) (Figure V.4). Les concentrations en phosphore seraient un déclencheur de la reproduction sexuée commun à *D. galeata* et *D. longispina*. A l'inverse, *D. galeata* présente un déclenchement de la reproduction sexuée plus sensible aux changements dans la pression de prédation et le réchauffement climatique que *D. longispina*.

Dans cette thèse, les modifications des communautés de cladocères ont été considérées comme un intégrateur de l'ensemble des impacts des perturbations sur la chaîne trophique pélagique. Les conclusions présentées sur la vulnérabilité des systèmes face au changement climatique ne concernent donc que la zone pélagique et n'englobent pas directement une vision écosystémique. Rares sont toutefois les études consacrées à la vulnérabilité des habitats littoraux ou benthiques (Vadeboncoeur et al. 2002).

Ce manque de considération résulte en partie du fait que les habitats benthiques sont encore trop souvent considérés seulement comme des sources ou des puits de nutriments pélagiques (Vadeboncoeur et al. 2002), en particulier dans les lacs profonds en dépit de leurs rôles parfois cruciaux dans le fonctionnement des lacs, au travers du recyclage des nutriments, du contrôle de la biomasse algale et du maintien des populations de poissons (e.g., Hecky et Hesslein 1995, Blumenshine et al. 1997, Vadeboncoeur et al. 2001, Vander Zanden et Vadeboncoeur 2002, Vander Zanden et al. 2006). Ces relations bidirectionnelles entre habitats pélagiques et benthiques (Covich et al. 1999, Palmer et al. 2000, Schindler et Scheuerell 2002) pourraient conduire à une vulnérabilité différente aux perturbations considérées.

V.3. La vulnérabilité de deux habitats lacustres face à un contexte de perturbations multiples

Tout comme les cladocères sont utilisés comme intégrateur des chaînes trophiques pélagiques, les chironomidés sont utilisés, au sein du programme de recherche IPER-RETRO, comme révélateurs des impacts des perturbations locales et régionales sur les réseaux trophiques benthiques (dans le cadre du travail doctoral de Victor Frossard, laboratoire Chrono-Environnement, Besançon).

Parmi les organismes benthiques des milieux lacustres, les chironomidés présentent l'avantage de produire des restes, qui s'archivent dans les sédiments, lesquels sont utilisés pour des reconstructions paléoécologiques comme nous l'avons mentionné dans le Chapitre I. La structure des communautés de chironomidés est fortement influencée par les changements dans le niveau d'oxygénation du fond des lacs (Quinlan et Smol 2000). Le basculement d'un état oxique à anoxique du fond des lacs résulte en partie d'une augmentation des apports en matière d'origine algale (i.e., matière produite mais non consommée) (Gray et al. 2002, Smtih et Schindler 2009, Dokulil et Teubner 2011), lesquels peuvent être modulés par les deux perturbations locales considérées dans cette étude. En soutenant une intense production phytoplanctonique, l'intensification des charges externes en phosphore peut accentuer le taux de sédimentation de matière organique algale vers le fond des lacs (Gray et al. 2002, Dokulil et Teubner 2011).

Cette augmentation de la quantité de matière organique algale sédimentée peut à son tour soutenir un métabolisme microbien plus important lequel peut amplifier les conditions d'anoxie au fond des lacs (Dokulil et Teubner 2011). D'autre part, le contrôle descendant des populations piscicoles sur les herbivores planctoniques peut à son tour modifier leur taux de broutage sur les communautés phytoplanctoniques (Peters et Dowing 1984) et donc les flux de sédimentation directe de matière algale. Le réchauffement climatique peut également influencer l'apparition de conditions anoxiques dans le fond des lacs, soit par des processus directs sur les propriétés physiques de la colonne d'eau (augmentation de la stabilité de la colonne d'eau et réduction du brassage hivernal, avec des conséquences sur l'isolation physique de l'hypolimnion et la limitation du renouvellement de l'oxygène dans les zones profondes) (e.g., Stefan et al. 1996, Straile et al. 2003, Jankowski et al. 2006, Blenckner et al. 2007), soit par des processus indirects sur la structure des communautés planctoniques (Jeppesen et al. 2009, Paerl et Huisman 2009).

Les reconstructions paléolimnologiques des communautés de chironomidés à l'échelle du siècle sur les lacs du Bourget et d'Annecy réalisées par Victor Frossard ont fait l'objet d'analyses comparables à celles réalisées sur les cladocères. Ces résultats préliminaires montrent de profondes modifications dans la trajectoire des communautés de chironomidés des zones profondes des deux lacs au cours du temps, en réponse aux trois perturbations environnementales marquées par :

- (i) une transition d'une communauté d'espèces oxyphiles (e.g., *Micropsectra* sp.) vers des espèces plus tolérantes des conditions hypoxiques (e.g., *Sergentia* sp.) dès le début des périodes d'eutrophisation (à partir des années 1940), témoignant du développement rapide de conditions anoxiques au fond des deux lacs,
- (ii) le maintien des communautés typiques de conditions hypoxiques lors de la ré-oligotrophisation dans les deux lacs.

Les méthodes multivariées d'ordination et de hiérarchisation des facteurs montrent que, tout comme les cladocères, les communautés de chironomidés ont répondu à l'ensemble des forçages locaux et globaux (Figure V.5). La période de temps principalement ciblée ici, commence à partir des années 1980 (correspondant à la période de ré-oligotrophisation des lacs). Ces années marquent le début d'une augmentation significative de la température de l'air (Chapitre III). Durant cette période, la trajectoire écologique des communautés de chironomidés est liée à la vulnérabilité des communautés pélagiques face aux perturbations environnementales.

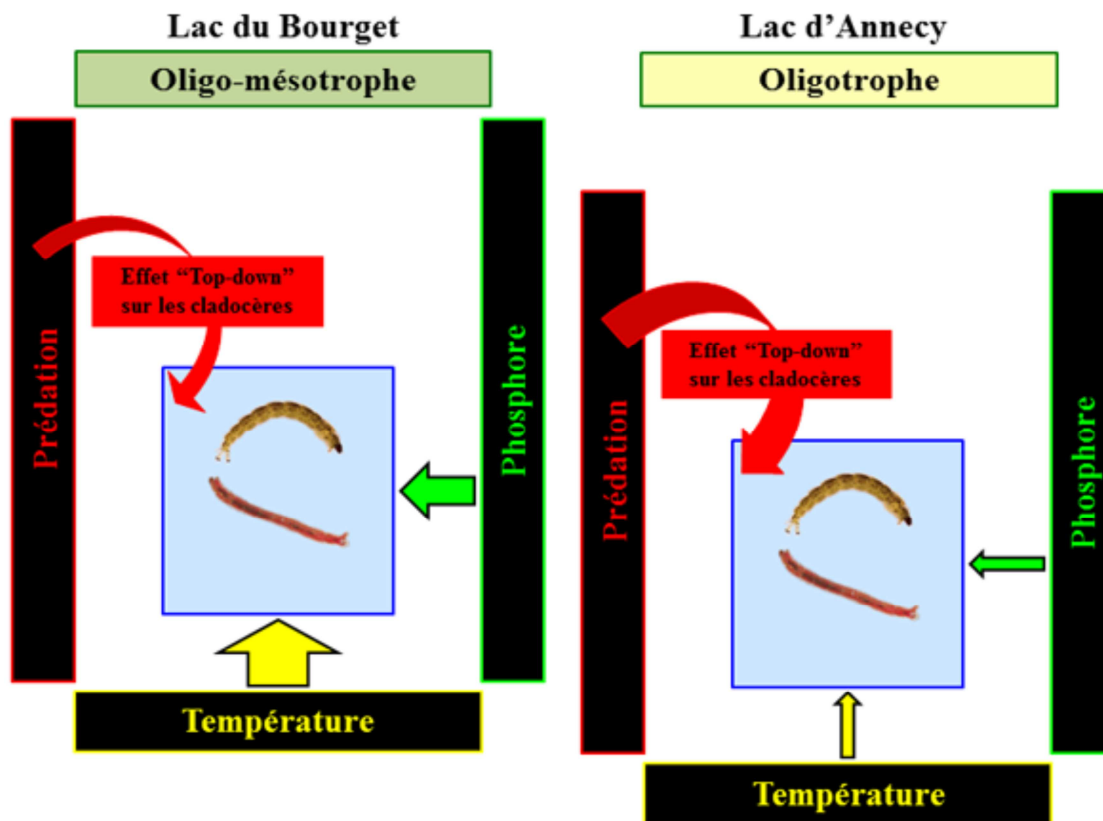


Figure V.5. Schéma récapitulatif de l'impact des trois perturbations environnementales sur les communautés de chironomidés des zones profondes des lacs du Bourget et d'Annecy. L'épaisseur des flèches correspond à l'intensité de la contribution de chaque perturbation environnementale dans la variance des communautés de chironomidés selon les résultats des GAM.

Plus précisément, dans le lac d'Annecy l'impact des changements dans le contrôle descendant des populations piscicoles sur les cladocères pélagiques (Chapitre III) influence plus fortement les communautés de chironomidés que dans le lac du Bourget (Figure V.5). Durant la période de ré-oligotrophisation du lac d'Annecy, les communautés de cladocères pélagiques sont principalement influencées par le contrôle descendant des populations de poissons (régulé par les pratiques de gestion piscicole) (Chapitre III). Dans le lac du Bourget, c'est le réchauffement climatique et le statut trophique qui contrôlent le plus les communautés de cladocères pélagiques (Chapitre III). Le couplage pélagique-benthique est donc plus influencé par les modifications du contrôle "top-down". En outre, durant cette période les sensibilités au réchauffement climatique des communautés de cladocères pélagiques et de chironomidés sont dépendantes d'un même forçage local (i.e., le statut trophique des lacs). En effet, la réponse de ces deux communautés au réchauffement climatique est plus forte dans le lac du Bourget, plus eutrophe que le lac d'Annecy. Cependant, un impact significatif du réchauffement climatique sur les communautés de chironomidés est observé dans le lac d'Annecy alors qu'aucun impact significatif n'était enregistré pour les communautés de cladocères pélagiques (Chapitre III). Ceci suggère une plus forte sensibilité des communautés benthiques au réchauffement climatique que les communautés pélagiques dans des conditions environnementales similaires à celles du lac d'Annecy. La sensibilité des communautés de chironomidés au réchauffement climatique dans le lac d'Annecy résulterait d'un impact plus important de l'augmentation de la stratification thermique de la colonne d'eau.

V.4. Perspectives

Les résultats obtenus au cours de ce travail de thèse dégagent certaines perspectives. En effet, suite aux résultats montrant que la vulnérabilité et la réponse des communautés pélagiques au réchauffement climatique est dépendante de l'intensité des perturbations locales, il est important d'inclure le rôle de ces perturbations dans la prédiction de l'impact futur des changements climatiques sur les écosystèmes lacustres. Cependant, la nature et la pertinence des estimateurs utilisés pour reconstruire les perturbations dans les approches paléolimnologiques se pose.

Dans le cas du phosphore, une homogénéisation de son estimateur entre les lacs (en utilisant par exemple la composition en isotope stable de l'azote de la matière organique sédimentaire) permettrait d'affiner nos modèles et d'estimer avec une plus grande robustesse l'impact des changements temporels des concentrations en phosphore sur le compartiment pélagique des grands lacs profonds. Pour l'intensité de la planctivorie des poissons, bien que nos résultats montrent que la taille des Daphnies peut être considérée comme un estimateur relativement fiable, l'influence d'interactions complexes entre le réchauffement climatique, la pression de prédation et les nutriments sur la taille des cladocères demande d'être approfondie. Le lac Léman fait l'objet, depuis 1957, d'un suivi annuel (échantillonnage tous les mois) de la qualité des eaux (SOERE). Dans ce suivi, le dénombrement de différents taxons zooplanctoniques (dont les Daphnies) est effectué. La mesure des tailles Daphnies peut également être réalisée sur l'ensemble de la période de temps du suivi. Les méthodes multivariées d'ordination et de hiérarchisation des facteurs utilisées durant cette thèse pourraient être appliquées sur ces données de taille, ce qui permettrait de déterminer la part des perturbations locales et régionales dans le contrôle des changements en taille des Daphnies.

La sensibilité spécifique selon le lac des compartiments pélagiques au réchauffement climatique et ce, en lien avec les différentes intensités des perturbations locales, pose la question d'une possible généralisation de ces tendances à l'échelle des grands lacs profonds des régions tempérées. Pour aborder ce point, l'ajout d'autres grands lacs profonds à notre jeu de lacs originel peut être envisagé. Un jeu de lacs peut être avancé comprenant le lac de Constance, le lac Majeur, le lac des Quatre-Cantons (Lake Lucerne), le lac Brienz, le lac Thun et le lac Walensee. Ces lacs se trouvent dans une même aire géographique suggérant une évolution du réchauffement climatique similaire à nos trois lacs d'étude. De plus, ces lacs sont soumis aux perturbations locales selon des intensités variables.

En parallèle, le couplage pélagique-benthique et la différence de sensibilité des deux compartiments au réchauffement climatique comme une fonction de l'intensité des perturbations locales suggèrent qu'une approche intégrée (i.e., couplage de l'étude des compartiments pélagiques et benthiques) peut être une future voie d'étude pour avoir une vision plus écosystémique de la sensibilité des lacs à un contexte de perturbations multiples.

Pour finir, ce travail de thèse a montré, plus spécifiquement pour les populations de Daphnies, que leurs comportements de reproduction sont influencés par l'ensemble des perturbations locales et régionales avec l'apparition d'événements d'hybridation interspécifique dans les lacs Léman et du Bourget. Ces événements d'hybridation seraient liés à un déclenchement de la reproduction sexuée par *D. galeata* et *D. longispina* en réponse à une même perturbation (le statut trophique du lac) ou à des sensibilités différentes entre les deux espèces aux autres perturbations (le réchauffement climatique et la pression de prédation). Pour améliorer notre compréhension de la nature des déclencheurs de l'hybridation interspécifique, il serait utile de comparer les périodes de production de femelles sexuées de *D. galeata* et de *D. longispina* ainsi que de mâles, en utilisant les données du suivi du lac Léman. Les analyses génétiques effectuées dans le chapitre IV peuvent être appliquées aux femelles sexuées de Daphnies afin d'identifier leur origine spécifique. La présence de deux génotypes mitochondriaux au sein d'une même espèce (*D. longispina*) soulève des questions traitant de la spéciation. Une étude expérimentale a montré une relation entre l'activité mitochondriale et l'ajustement de la tolérance thermique d'organismes aquatiques (Sommer et Pörtner 2002) suggérant que des individus présentant des génotypes mitochondriaux différents pourraient occuper des niches écologiques distinctes. Par conséquent, est-ce qu'il y a un rôle écologique à une telle différence au niveau du génotype mitochondrial des deux groupes de *D. longispina* ? Ces différences dans les génotypes mitochondriaux des deux groupes de *D. longispina* peuvent-elles former des barrières pré- ou post-zygotiques empêchant une reproduction intergroupe ? La détermination de la distance génétique entre les deux groupes apporterait des éléments de réponse. Une faible distance génétique signifierait un échange de gènes fréquent entre les deux, avec la réciproque pour une grande distance génétique. La détermination des distances génétiques peut se faire par le calcul du déficit d'hétérozygotes (F_{st}) qui est un indice de diversification des populations. En abritant uniquement *D. longispina*, le lac d'Annecy serait un bon modèle pour aborder de telles questions. Cependant, la taille de notre jeu de données dans ce lac, i.e. la quantité d'éphippies pour chaque groupe de *D. longispina*, n'est pas suffisante pour pouvoir calculer un tel indice. Cependant, un échantillonnage mensuel sur une année permettrait de constituer un jeu de données adéquat pour calculer cet indice.

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