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L'INFLUENCE HUMAINE EN RELATION AVEC LES CHANGEMENTS ENVIRONNEMENTAUX: ÉVOLUTION DES LACS EN NOUVELLE-ANGLETERRE RECONSTITUÉE PAR L'ANALYSE DES DIATOMÉES

Thèse
présentée
à la Faculté des études supérieures
de l'Université Laval
pour l'obtention
du grade de Philosophiae Doctor (Ph.D.)

FACULTÉ DE FORESTERIE ET GÉOMATIQUE
UNIVERSITÉ LAVAL
QUÉBEC

JUILLET 2004

Résumé

Dans la présente recherche, l'influence humaine et climatique des 1500 dernières années sur quatre lacs de Nouvelle-Angleterre (États-Unis) a été reconstituée par l'analyse des diatomées fossiles provenant des sédiments. Différentes méthodes ont été testées pour inférer certaines variables environnementales à l'aide des diatomées. Les méthodes des moyennes pondérées et de la probabilité maximale se sont avérées les plus appropriées pour la reconstitution des variables du gradient principal, tandis que les réseaux neuronaux artificiels et la probabilité maximale sont préférables pour les variables du gradient secondaire. Différentes transformations des données sont appropriées pour chacune des méthodes. Les diatomées fossiles des lacs ont enregistré un patron régional propre à la déforestation suite à la colonisation par les Européens. Malgré le rétablissement des forêts autour des sites depuis 1900 AD, trois lacs montrent à l'état actuel des conditions qui ne correspondent pas à celles de la période avant-perturbation. Ceci est dû aux caractéristiques locales des sites, tels que l'évolution naturelle des lacs, les perturbations naturelles (ouragans), ainsi que le développement des marais. Pour rétablir l'état « naturel » théorique envisagé dans la restauration, il est donc important de tenir compte de l'évolution naturelle des lacs. Au lac Walden Pond (Massachusetts), un enrichissement accéléré en nutriments a été inféré suite à l'usage récréatif intensif depuis env. 1950 AD. Depuis 1975 AD, le taux d'eutrophisation a diminué grâce aux mesures de gestion. L'état naturel du lac reconstitué par notre étude représente un bon guide pour les futures mesures de gestion. Au lac Levi Pond (Vermont), une tendance accrue à l'humidité pendant les dernières 2000 années, qui correspond au refroidissement global du Néoglaciaire, a été inférée par les diatomées. Les diatomées sont donc d'une utilité potentielle pour les études paléohydrologiques dans les régions tempérées. L'analyse mensuelle de la flore diatomifère dans Bates Pond (Connecticut), a indiqué que les assemblages sont liés à la stratification, ce qui a permis d'identifier une période de mélange prolongée dans le passé à partir des assemblages fossiles. Le maximum de productivité diatomifère en automne indique que c'est la saison privilégiée pour l'échantillonnage d'eau en vue du développement des modèles d'inférence. Cette thèse apporte des nouvelles connaissances sur l'évolution et l'écologie des lacs en Nouvelle-Angleterre, et sur deux aspects méthodologiques pertinents pour la discipline de la paléolimnologie.

Abstract

The human and climatic impact on four New England lakes was reconstructed by analysis of fossil diatoms preserved in lake-bottom sediments. Different diatom-based methods for the reconstruction of environmental variables (pH, total phosphorus, alkalinity) were tested. Weighted averaging and Gaussian logit regression were the most appropriate methods for the reconstruction of variables representing the principal gradient, whereas artificial neural networks and Gaussian logit regression performed better for secondary gradient variables. It was shown that different data transformations may be useful for different reconstructions. Fossil diatom assemblages of the sites recorded a regional pattern of deforestation and agricultural activity following European settlement. Despite the re-establishment of forests in the lake watersheds since 1900 AD, three lakes did not return to pre-disturbance conditions. This is due to local site characteristics, such as natural lake evolution, local natural disturbance patterns (hurricanes), and peatland development. It is therefore important to consider the natural dynamics of lakes when establishing the theoretical « natural » state for restoration purposes. At Walden Pond, Massachusetts, an accelerated nutrient enrichment was inferred from 1950 AD onwards, related to intensive recreational use of the lake. Since 1975 AD, the rate of eutrophication has diminished after management measures were implemented. The natural state of the lake reconstructed by this study represents a useful benchmark for future management decisions. In Levi Pond, a trend of increasing humidity during the past ca. 2000 years has been inferred by diatoms, corresponding to the period of Neoglacial cooling. This result indicates that diatoms may be a useful tool for future paleohydrological studies in temperate regions. The seasonal study of diatoms in Bates Pond, Connecticut, indicated that diatom assemblages are strongly influenced by stratification, which helped to identify a period of prolonged full-circulation in the past based on the fossil assemblages of the same lake. The maximum diatom productivity in autumn indicated that this is the most appropriate season for taking water samples for diatom inference model development. This thesis has provided new knowledge of the evolution of New England lakes before and after European settlement and on two pertinent methodological aspects of paleolimnologic study.

Avant-Propos

Cette thèse est composée de 6 chapitres dont 4 sont présentés sous forme d'articles qui en sont à différentes étapes dans le processus de publication. Ma contribution et celle de chaque co-auteur aux articles sont détaillées ci-dessous. Le sixième chapitre contient un résumé et une discussion générale se rapportant aux résultats des chapitres 3 à 5. Il ne figure donc pas dans cette liste.

Chapitre 2

Dörte Köster, Julien Racca et Reinhard Pienitz. 2004. Diatom-based inference models and reconstructions re-visited : methods and transformations. Journal of Paleolimnology 32 (3) : 13pp.

Cet article a été accepté pour publication le 9 mars 2004.
Les données analysées dans ce chapitre ont été fournies en partie par Sushil Dixit (Environment Canada, National Guidelines & Standards Office, Ottawa, Ontario). J'ai effectué les analyses statistiques et les reconstitutions quantitatives avec des modèles différents et j'ai préparé le manuscrit. Julien Racca a développé les modèles basés sur les réseaux neuronaux artificiels, a effectué les reconstitutions avec cette méthode et a calculé les biais pour tout les modèles. Reinhard Pienitz a fourni le financement pour cette étude et a contribué à la rédaction.

Chapitre 3

Dörte Köster, Brent Wolfe, Reinhard Pienitz, Sylvia Barry, David Foster, et Sushil Dixit. Paleolimnological assessment of human-induced impacts on Walden Pond (Massachusetts, USA) using diatoms and stable isotopes. Soumis au journal « Aquatic Ecosystem Health and Management » (Taylor and Francis, Philadelphia).

Ce manuscrit a été soumis en juillet 2003.
J'ai fait l'analyse des diatomées et l'énumération des chrysophycées, ainsi que les reconstitutions quantitatives des variables environnementales. J'ai préparé la majorité du manuscrit. Brent Wolfe a analysé les isotopes stables et la géochimie et a écrit les sections concernant ses méthodes et ses résultats. Reinhard Pienitz a contribué à la rédaction et au

financement de cette étude. Sylvia Barry a pris la carotte de sédiment avec d'autres employés de Harvard Forest, a établi la chronologie et a contribué aux données historiques. David Foster a fourni les analyses de pollens, a contribué à la rédaction et au financement de l'étude. Sushil Dixit a fournit les données pour le développement des fonctions de transfert utilisées dans ce chapitre.

Chapitre 4

Dörte Köster et Reinhard Pienitz. Environmental history of two New England ponds: natural dynamics versus human impacts. En préparation.

Ce manuscrit est prévu pour la soumission au journal « The Holocene ».
Les carottes prélevées pour cette étude l'ont été par différents chercheurs de Harvard Forest (Petersham) qui ont aussi effectué les analyses de perte au feu (Elaine Doughty, Wyatt Oswald), les analyses des pollens (Susan Clayden, J. McLaughlin) et la datation des sédiments (Sylvia Barry). J'ai réalisé les analyses des diatomées fossiles, les reconstitutions quantitatives des variables environnementales et la rédaction du manuscrit. Reinhard Pienitz a contribué à la rédaction et a fournit le support financier.

Chapitre 5

Dörte Köster et Reinhard Pienitz. Seasonal diatom variability and paleolimnological inferences - a case study. En preparation.

Ce manuscrit est prévu pour la soumission au journal « Freshwater Biology ».
J'ai planifié, supervisé et en partie assuré les travaux de terrain pour l'expérience des pièges de sédiment. J'ai participé au prélèvement de la carotte de sédiment. J'ai analysé les diatomées récentes et fossiles, j'ai effectué les analyses statistiques et j'ai préparé le manuscrit. Sylvia Barry a réalisé la majorité des travaux de terrain. Reinhard Pienitz a contribué à la rédaction du manuscrit et au financement. Les chercheurs de Harvard Forest ont fournit de l'aide logistique, les datations et les résultats de perte au feux.

Remerciements

Tout d'abord je tiens à remercier Reinhard Pienitz, mon directeur de recherche, de m'avoir proposé ce sujet de thèse et d'avoir facilité mes démarches d'administration, surtout après mon arrivé à Québec. Sa disponibilité immédiate était d'une grande aide tout le long de mon doctorat. J'ai beaucoup apprécié sa façon amicale et en même temps professionnelle de diriger ma recherche, son ouverture et son support pour les projets connexes, comme l'étude de saisonnalité et le stage en Norvège. Merci aussi pour les bons moments partagés que ce soit sur les terrains de recherche ou de soccer.

Je remercie les membres du comité de thèse, Warwick Vincent et Matthew Hatvany, pour leur aide dans les sujets hors paléolimnologie. Les discussions avec Warwick m'ont aidé a mieux comprendre la limnologie dans sa complexité et Matthew était là pour m'assister dans la recherche de données historiques.

Je remercie David Foster pour la mise en place du projet pluridisciplinaire dont cette thèse faisait partie et pour sa contribution au chapitre sur Walden Pond. Ce projet m'a donné la chance de rencontrer et travailler en équipe avec des autres chercheurs impliqués, ce qui a été une expérience enrichissante. Parmi eux, je suis très reconnaissante envers Sylvia Barry, qui a coordonné les études du projet, a assuré une grande partie des travaux de terrain, surtout pour notre expérience des pièges de sédiment, et les datations. Son efficacité, son ouverture et sa belle personnalité m'ont rendu la collaboration avec Harvard Forest très agréable. Un grand Merci à Brent Wolfe, qui a contribué à l'acquisition des données des isotopes stables et de la géochimie pour quelques lacs et avec qui j'ai partagé des discussions intéressantes ainsi qu'une co-rédaction efficace. Je remercie Donna Francis pour les discussions sur les données des chironomides et Sushil Dixit d'avoir fourni les données des 82 lacs en Nouvelle-Angleterre pour le développement des fonctions de transfert.

Un grand Merci à John Birks de m'avoir permis d'effectuer un stage dans l'Institut de Botanique à Bergen, Norvège. Je le remercie pour son accueil affable, ses instructions tout à fait claires dans les problématiques qui m'avais paru plutôt obscures auparavant, et pour son encouragement dans un projet qui a finalement mené à la rédaction d'un article. Plusieurs personnes sur place ont rendu mon séjour à Bergen inoubliable, dont Jorunn par son invitation sur le terrain et les bonnes discussions sur les diatomées, Kari sur le coté administratif, Annette par l'initiation au Tango, ainsi que Khem et tout les autres étudiants « Marie-Curie » par le partage quotidien de la vie norvégienne.

Cette thèse n'aurait pas été possible sans l'aide et support quotidien de l'excellente équipe du laboratoire Paléolimnologie-Paleoécologie. Merci à Tam pour le partage de ses connaissances scientifiques, mais surtout pour son amitié et tout les bon moments en plein air. Merci à Sonja pour l'idée du projet de saisonnalité et l'aide à sa réalisation, de la bonne collaboration quotidienne, de son support dans les moments difficiles et son amitié. Merci à Claudia pour l'aide infini quant au traitement des échantillons, mais aussi et surtout pour tout les petits trucs et des bonnes discussions qui rendent le travail dans un labo agréable. Merci à Marie-Andrée de partager ses connaissances de statistiques, de fournir les données du modèle pour le carbone organique dissout et de son attitude positive contagieuse. Merci à Julien pour les discussions fructueuses et la bonne collaboration pour chapitre 2, et à Émilie, Karin et Murray qui ont facilité mon intégration au labo au début et ont toujours été là ensuite pour la correction des articles et les discussions intéressantes.

Je remercie la « Ginetti Family », les propriétaires de Bates Pond, et surtout madame Ginetti, pour leur permission d'accéder régulièrement à leur terrain pour l'expérience des pièges de sédiment et pour le carottage. Leur accueil chaleureux a fait ressembler les sorties de terrain à des visites de famille. Thanks for the tea and cake!

Quant au développement personnel pendant le doctorat, auquel j'accorde au moins une aussi grande importance qu'à l'avancement professionnel, je dois une très grande part à mes amis du CEN et du groupe de course à pied. Surtout les échanges enrichissants avec Fabrice m'ont beaucoup inspiré et ouvert l'esprit et sa complicité a été une grande source d'énergie. Un grand merci à Céline pour son amitié et son support. Merci à tout les autres d'avoir partagé de l'implication dans la vie associative, les bons moments conviviaux et les projets artistiques. Merci aux amis de sport et de plein air de m'avoir rendu possible et d'avoir partagé toutes les belles expériences sur et hors piste.

À cette occasion, j'aimerais aussi remercier Thomas Hübener, mon co-directeur de maîtrise en Allemagne, pour m'avoir initié au monde des diatomées, pour avoir établi le contact avec Reinhard, et pour sa disponibilité continue jusqu'au présent dans les questions algales.

Ma curiosité scientifique a été grandement soutenue par mes parents, qui m'ont toujours encouragée dans mes projets, et aussi dans ce dernier malgré mon absence prolongée. Je les remercie beaucoup pour tout leur support sans lequel je ne me serais jamais rendu jusqu'ici.

Merci à Eric pour sa confiance inconditionnelle dès le début, son écoute, son grand support moral durant la période critique de rédaction, et pour l'aide à la rédaction en français.

Le support financier pour cette étude a été fourni par la National Science Foundation, Etats-Unis (subvention no. 9903792 accordée à David Foster), par les subventions du Conseil de Recherche en Sciences Naturelles et en Génie du Canada (CRSNG), attribuée à Reinhard Pienitz, par une bourse de l'Union Européenne « Marie-Curie », qui m'a été attribuée, et par le Fonds de soutien du Département de Géographie de l'Université Laval. Le support logistique a été offert par le Centre d'études nordiques et Harvard Forest.

Für Gerda

Croyez ceux qui cherchent la vérité, doutez
de ceux qui la trouvent."

André Gide (1869-1951)

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1 Introduction générale

La compréhension de la dynamique naturelle des écosystèmes est une nécessité pour une meilleure évaluation des conséquences écologiques de l’activité anthropique et pour l'étude des écosystèmes récentes. Cette compréhension apportera également une aide à la gestion du territoire et à l’aménagement des paysages. Des recherches antérieures suggèrent que les changements de végétation en Nouvelle-Angleterre au cours des derniers siècles, jusqu’à présent expliqués par l’influence humaine, soient plutôt une continuation ou une modification des tendances initiées lors des variations climatiques induites par le “Petit Âge Glaciaire” (env. 1550 – 1850 AD) (Gajewski 1987; Russell et al. 1993; Fuller et al. 1998). Jusqu’à présent, les études régionales ont mis l’accent soit sur les effets continus de l’activité humaine sur les écosystèmes soit sur l’analyse du développement naturel des écosystèmes durant l’Holocène. Pourtant, aucune étude compréhensive des effets de la perturbation lié à l'activité anthropique dans le contexte des changements climatiques des dernières siècles n’a été menée.

La question principale qui se pose est donc la suivante: quels facteurs environnementaux et anthropiques ont provoqué les changements végétaux en Nouvelle-Angleterre pendant les dernières 1500 années ? Nous proposons l'hypothèse que ces changements aient été initiés par la variabilité climatique du Petit Âge Glaciaire et qu’ils aient connu un renforcement par l’influence des colons lors des derniers siècles.

Pour tester cette hypothèse, une étude paléoécologique pluridisciplinaire a été mis sur pied par David Foster et Janice Fuller de l’université Harvard (Harvard Forest) qui a été appuyée par la National Science Foundation (Etats-Unis). Cette étude vise à vérifier plus précisément les effets du "Petit Âge Glaciaire" par rapport aux effets de l’activité humaine sur la dynamique des forêts en Nouvelle-Angleterre pendant les derniers 1500 ans, en employant des indicateurs indépendants de climat et de l’activité humaine (pollens, diatomées, chironomides, isotopes stables). L'analyse des diatomées dans les séquences sédimentaires de quatre lacs en Nouvelle-Angleterre s'inscrit dans ce projet et est le sujet principal de cette thèse de doctorat. L’étude des diatomées permet de reconstituer les anciens environnements lacustres qui reflètent des changements climatiques et historiques de leur bassin versant. Deux études de nature méthodologique complémentaire sont effectuées afin d'améliorer et approfondir les interprétations qualitatives et quantitatives tirées des données recueillies.

1.1 Région : paysages et aperçu historique

La région d'étude inclut les états du Vermont, du New Hampshire, du Massachusetts et du Connecticut, au nord-est des États-Unis, qui forment avec le Maine et le Rhode Island la Nouvelle-Angleterre. La région est composée de sept ensembles physiographiques principales: les plaines côtières, les montagnes intérieures, la vallée de la rivière Connecticut, la vallée Champlain, les Montagnes Blanches, les Montagnes Vertes, et les Montagnes Taconiques. La géologie est dominée par les roches granitiques et gneissiques d'âge paléozoïque (Denney, 1982) ainsi que par un sol acide pauvre en nutriments. La vallée Connecticut constitue une exception puisqu'elle contient des sédiments glaciaires, du sable deltaïque et des dépôts d'inondations. Le climat est tempéré et varie d'une région à l'autre en fonction des gradients d'altitude et de la distance à l'océan (Foster, 1995). La végétation change en fonction de la latitude et de l'altitude. Au Vermont, au New Hampshire ainsi qu'au nord du Massachusetts, on trouve la forêt feuillue nordique composée en partie des conifères, tandis qu'au sud de la Nouvelle-Angleterre se situe la forêt feuillue centrale. La dynamique naturelle des écosystèmes en Nouvelle-Angleterre est contrôlée par les changements climatiques et les perturbations naturelles, tels que les feux, les ouragans, les inondations et les pathogènes (Foster 1995; Foster et al. 1998a).

L'influence humaine sur les forêts en Amérique du Nord a commencé longtemps avant l'arrivée des Européens (Russell, 1983). Des données archéologiques indiquent un gradient régional de la population amérindienne en Nouvelle-Angleterre : décroissant à partir des régions du sud et de la côte vers le nord, et décroissant à partir des bassins fluviaux vers les montagnes (Patterson et Sassaman, 1988 dans Foster, 1995). Les documents historiques et archéologiques indiquent que les Amérindiens de la Nouvelle-Angleterre ont surtout vécu de la chasse et de la pêche, mais qu'ils ont aussi pratiqué l'agriculture à coté des villages saisonniers, au bord des grandes rivières et de la mer (Day 1953). Un changement de la végétation dû aux feux initiés par les autochthones a été mis en évidence dans Crawford lake en Ontario (Clark et Royall 1995). En Nouvelle-Angleterre, toutefois, il n'y a pas d'évidence claire que les Amérindiens ont brûlé des grands territoires forestiers (Russell 1983). Jusqu'à date, il n'y a pas d'indice qu'il y ait eu une perturbation des écosystèmes en Nouvelle-Angleterre dû à l'activité amérindienne (Foster 1995).

Arrivés en Nouvelle-Angleterre au 16e siècle, les colons européens ont migré vers le nord et l'intérieur du pays, en partant des habitations côtières bien établies (Foster, 1995). La première expansion démographique s'est produite le long des vallées des rivières à la fin du 17e siècle. Les montagnes au nord-ouest et les Montagnes Vertes ont été les dernières régions colonisées vers 1820 AD. Les colons ont connu différentes phases économiques et démographiques. Au début de la période coloniale (1600 à 1840 AD), l'agriculture de basse intensité et la production artisane étaient l'occupation principale des habitants. Vers la fin de la période coloniale, une économie de marché s'est développée sur la base d'une agriculture intensive et commerciale (Garrison, 1995, dans Foster 1995) avec une densité de population maximale dans les villes de montagne (Wilson, 1855; Raup et Carlson, 1941, dans Foster, 1995). Pendant la période industrielle, datant approximativement des décennies suivant 1850 AD, une migration significative des habitants des villages vers les villes industrielles situées dans les vallées et vers l'ouest américain s'est produite ayant eu comme conséquence l'abandon de vastes territoires en Nouvelle-Angleterre (Barraclough et Gould, 1955, dans Foster, 1995). Au cours du dernier siècle, la forêt, qui avait envahie les terres abandonnées, fut exploitée avec une production maximale en 1909-1910 AD (Hawes, 1953, dans Foster, 1995). Durant la deuxième moitié du 20e siècle (période post-industrielle), l'occupation du territoire a été caractérisée par le développement des banlieues près des grandes villes, par la croissance du marché des maisons secondaires et par un accroissement de l'activité récréative, notamment aux bords des lacs.

1.2 Influence humaine sur les lacs

La déforestation, l'agriculture, l'usage récréatif des milieux aquatiques et le développement urbain dans les bassins versants ont affecté la qualité de l'eau de nombreux lacs en Nouvelle-Angleterre. (Siver et al. 1996; Dixit et al. 1999; Siver et al. 1999; Francis et Foster 2001). Les changements dans les assemblages fossiles de diatomées lacustres ont démontré un enrichissement en nutriments de l'eau suite à la déforestation et au développement urbain en Nouvelle-Angleterre (Davis et Norton 1978). Les reconstitutions quantitatives basées sur les diatomées ont indiqué l'augmentation des concentrations de phosphore total (TP) et d'azote (TN) (Dixit et al. 1999; Siver et al. 1999) et du pH et de l'alcalinité (Davis et al. 1994a) depuis la colonisation par les Européens. Pendant que l'impact humain sur les lacs est bien étudié, peu d'information existe sur la façon dont les lacs récupèrent après que la forêt s'est rétablie dans les bassin versants des lacs (Francis et Foster 2001). Avec la réinstallation de la forêt, la composition végétale ne s'est pas rétablie, ce qui indique que d'autres facteurs, comme la coupe forestière, les maladies forestières, les ouragans et la suppression des feux, continuent d'influencer les bassins versants (Fuller et al. 1998; Francis et Foster 2001). Il reste à vérifier comment les lacs répondent à l'arrêt des perturbations majeures dans leur bassin versant.

Une autre perturbation d'origine anthropique sont les dépôts d'acides qu'ont reçu les lacs et leur basin versant depuis la fin du 19e siècle (Charles 1990) jusqu'à aujourd'hui (Stoddard et al. 1999). Un nombre considérable de lacs a connu une acidification liée au dépôt atmosphérique des acides forts, par exemple dans les montagnes Adirondacks (Charles 1990; Cumming et al. 1994), en Nouvelle-Angleterre (Davis et al. 1994a) et dans la région de Sudbury, Canada (Dixit et al. 1992a). Des lacs possédant un faible pouvoir de tampon peuvent également connaître une acidification naturelle lente et graduelle durant tout l'Holocène (Ford 1990; Rhodes et Davis 1995). Par contre, beaucoup de lacs au Connecticut possèdent un pourvoir tampon élevé ainsi que des mécanismes de formation de l'alcalinité suffisants pour ne pas être acidifiés suite à des dépôts d'acides atmosphériques (Siver et al. 1999, 2003). En résumé, l'acidification est un facteur qui affecte différemment les lacs de la Nouvelle-Angleterre, et il est donc important d'en tenir compte lorsque les lacs de cette région sont étudiés.

1.3 Petit Âge Glaciaire

Avant l'arrivée des Européens, des changements dans la composition de la forêt en Nouvelle-Angleterre ont été observés, quoique les causes ne soient pas claires. Ces changements sont survenus pendant une période de refroidissement global, connue sous le nom du Petit Âge

Glaciaire. Pendant cette période, l'hémisphère Nord a connu des conditions plus froides avant le 20e siècle, surtout au milieu du 17e et du 19e siècle (Bradley et Jones 1993; Overpeck et al. 1997; Mann et al. 1998). Cependant, le climat qui régnait pendant le Petit Âge Glaciaire était plutôt variable, et l'ampleur et la chronologie des changements diffèrent d'une région à l'autre (Williams et Wigley 1983; Grove 1988; Bradley et Jones 1993; Bradley 2000). En Amérique du Nord, les indices d'un refroidissement et/ou d'une augmentation de l'humidité pendant le Petit Âge Glaciaire sont basés sur des études de carottes de glace (Naftz et al. 1996) et de cernes de bois (Payette et al. 1989; d'Arrigo et Jacoby 1992; Lavoie et Payette 1992), sur des analyses anthracologiques (Clark 1990) et sur des analyses polliniques des sédiments lacustres (Grimm 1983; Gajewski 1988; Brugam et Swain 2000). À une échelle temporelle plus large, le Petit Âge Glaciaire représente une accélération d'un refroidissement à long terme, le Néoglaciaire, qui a suivit l'optimum climatique au milieu de l'Holocène, vers 4000 ans BP (Gajewski 1988).

Les enregistrements d'un effet direct du Petit Âge Glaciaire sur les écosystèmes aquatiques en Amérique du Nord sont plutôt rares et souvent situés dans les environnements extrêmes. À la limite des arbres du Nord du Québec, une augmentation du niveau d'eau d'un lac causé par une humidité accrue a été observée au 18e siècle (Payette et Filion 1993). Dans le haut arctique canadien, les assemblages diatomifères d'un lac ont connu une augmentation de leur diversité pendant le Petit Âge Glaciaire (Wolfe 2003). Les reconstitutions quantitatives pour la même région et réalisées à l'aide de modèles d'inférence basés sur les diatomées ont indiqué un refroidissement et une baisse du pH à long terme pendant le Néoglaciaire avec un minimum de température pendant le Petit Âge Glaciaire (Joynt et Wolfe 2001; Wolfe 2002). Dans un lac salé dans les prairies américaines la salinité a baissé en 1200 AD ce qui indique une humidité élevée (Laird et al. 1996). Dans le Elk Lake, au Minnesota, une augmentation de l'abondance relative d'une diatomée vernale a indiqué que les précipitations hivernales et/ou les températures étaient plus basses entre 1450 AD et 1850 AD (Bradbury et Dieterich-Rurup 1993). Un changement similaire a été observé au Lac Baïkal, en Russie, où une diatomée estivale a remplacé une diatomée vernale indiquant un mélange printanier retardé et raccourci dû aux glaces plus épaisses suite aux précipitations hivernales élevées et aux températures basses (Edlund et al. 1995). En Nouvelle-Angleterre, aucun indice aussi important n'a été décelé pour le Petit Âge Glaciaire jusqu'à présent. Toutefois, des changements à plus long terme de niveau d'eau dans les lacs en Ontario (Yu et al. 1997), au Québec méridional (Lavoie et Richard 2000), au Maine (Almquist et al. 2001; Shuman et al. 2001) et au Massachusetts (Shuman et al. 2001) ont indiqué une augmentation de l'humidité au cours des derniers 2000 à 4000 ans, liée aux conditions plus froides et/ou humides pendant le Néoglaciaire.

En somme, l'évidence globale d'une époque climatique froide avant le réchauffement récent serait difficile à ignorer. Toutefois, les effets sur les écosystèmes étaient distincts ou parfois absents dans les différentes régions, de sorte que les interprétations des causes, de la nature et de la durée de cette période sont incomplètes et parfois contradictoires (Rind et Overpeck, 1993). De plus, l'influence humaine et les perturbations naturelles rendent l'interprétation des réponses des écosystèmes aux changements climatiques encore plus complexe. C'est le cas de la Nouvelle-Angleterre, avec, d'une part, l'implantation des Européens pendant le Petit Âge Glaciaire et, d'autre part, le fait d'être une région souvent affectée par le passage des ouragans. Il faut noter que peu d'études ont interprété les changements récents de la végétation en tenant compte de la variabilité naturelle avant la colonisation humaine et aucune étude n'a inclus des indicateurs paléoclimatiques indépendants pour interpréter la dynamique des écosystèmes à long terme (Russell et al. 1993; Fuller et al. 1998)

1.4 Modèles d'inférence et dynamique saisonnière des diatomées : considérations méthodologiques

La reconstitution quantitative des variables environnementales dans les lacs, comme prévue dans cette étude, est souvent effectuée à l'aide de modèles d'inférence ou de fonctions de transfert (voir la section méthodologie pour plus de détails). Les modèles disponibles pour la région d'étude utilisent la méthode des moyennes pondérées et les mêmes transformations de données pour toutes les variables (Dixit et al. 1999). Pourtant, une multitude de méthodes et de façons de manipuler les données (transformations) avant l'analyse est disponible pour les reconstitutions paléoenvironnementales (Birks 1995), dont une nouvelle méthode tout récemment introduite à la paléolimnologie, les réseaux neuronaux artificiels (RNA) (Racca et al. 2001). De plus, il est avantageux de tester différentes méthodes et, le cas échéant, d'établir des reconstitutions de « consensus » (moyenne de plusieurs reconstitutions différentes) afin de développer les modèles les plus appropriés pour chaque variable modélisée (Birks 1995). Toutefois, cette approche a rarement été adoptée dans les études paléolimnologiques (Korsman et Birks 1996; Hall et al. 1997) et les RNA n'ont pas encore été utilisés pour la reconstitution quantitative des variables environnementales dans les lacs. Dans notre étude, la performance statistique et la fiabilité de différents modèles d'inférence sont testées en comparant les reconstitutions avec des mesures de la chimie de l'eau récentes dans un des lacs (Köster et al. accepté). De cette manière on peut décider quelle est la meilleure méthode de reconstitution à utiliser dans les autres lacs.

Les fonctions de transfert appliquées dans l'étude paléolimnologique sont basées sur des échantillons de diatomées provenant de sédiments de surface, qui sont souvent reliés à une seule mesure ponctuelle des variables physico-chimiques de l'eau dont la date d'échantillonnage diffère entre les modèles. Toutefois, il est connu que les assemblages d'algues dans les lacs tempérés montrent une forte dynamique temporelle, provoquée par les variations saisonnières des propriétés physico-chimiques de l'eau (Sommer et al. 1986; Interlandi et al. 1999; Wetzel 2001). Pour cette raison, il est possible que certaines diatomées prolifèrent dans une saison autre que celle de l'échantillonnage de l'eau. Par conséquent, celles-ci peuvent être influencées par d'autres variables qui dominent pendant d'autres périodes de l'année. Il serait important à vérifier la saison durant laquelle les diatomées se trouvant dans les sédiments de surface ont effectué leur croissance et de déterminer ainsi la saison qui serait la plus appropriée pour prendre les mesures physiques et chimiques de l'eau qui serviront au développement des futurs modèles d'inférence.

Pour l'interprétation écologique des séquences fossiles des diatomées, les connaissances des préférences autécologiques des différentes espèces sont essentielles. Comme les réponses des populations à l'échelle saisonnière sont contrôlées par l'intégration physiologique des stimuli à haute fréquence spécifiques pour chaque taxon, l'étude des séquences saisonnières et leur relation avec l'environnement peut s'avérer utile pour obtenir des informations sur les préférences écologiques individuelles (Reynolds 1990). Selon notre connaissance, la dynamique saisonnière des algues a rarement été étudiée en vue de son implication pour les analyses paléolimnologiques (Siver et Hamer 1992; Bradbury et Dieterich-Rurup 1993;

Bennion et al. 2000; Lotter et Bigler 2000; Bradshaw et al. 2002), malgré que Smol (1990) ait souligné le besoin d'une communication accrue entre les écologistes et paléoécologistes.

1.5 Objectifs

L'objectif principal du travail présenté dans cet ouvrage est d'identifier et séparer les effets climatiques des effets anthropiques dans le bassin versant de quatre lacs de la Nouvelle-Angleterre lors des dernières 1500 années.

Les objectifs spécifiques de cette étude sont de :

- développer, à partir des données existantes, des modèles d'inférence basés sur les diatomées et évaluer la performance des différentes méthodes pour la reconstitution quantitative des variables environnementales;
- reconstituer de façon qualitative (par interprétation écologique des assemblages diatomifères fossiles) et quantitative (par l'application des fonctions de transfert) les conditions paléolimnologiques dans quatre lacs de la Nouvelle-Angleterre;
- identifier les facteurs principaux déterminant les changements saisonniers des assemblages de diatomées dans un lac et appliquer de telles informations à l'interprétation des diatomées fossiles dans le but d'évaluer les implications pour l'approche paléolimnologique en général;
- interpréter les changements lacustres du passé dans les lacs à l'égard des effets humains et climatiques en considérant nos résultats et ceux obtenus à travers d'autres analyses paléolimnologiques.

1.6 Intérêt et pertinence de l'étude

Les résultats de cette recherche seront d'un intérêt particulier pour les gestionnaires des ressources aquatiques naturelles dans la région d'étude, pour les chercheurs qui s'intéressent aux changements globaux et pour les paléolimnologistes. Les gestionnaires des ressources naturelles et les conservateurs ont besoin d'informations sur le statut naturel et la variabilité naturelle des écosystèmes avant l'arrivée des Européens, afin de pouvoir établir des directives réalistes pour la restauration et la gestion efficace des écosystèmes.

Deuxièmement, la compréhension des effets cumulatifs des changements climatiques et de l'influence humaine sur les écosystèmes est pertinente pour les écologistes et chercheurs impliqués dans la recherche sur les changements globaux.

Troisièmement, l'évaluation et l'amélioration des méthodes paléolimnologiques (par exemple par l'approfondissement du lien avec l'écologie « récente » et par l'évaluation de la performance des méthodes statistiques quantitatives) est d'un intérêt particulier pour les chercheurs impliqués dans ce champ d'étude et pour ceux qui mettent en application ces résultats.

1.7 Méthodologie

1.7.1 Sites d'étude

La localisation des quatre lacs à l'étude a été choisie pour maximiser les gradients de longitude, d'altitude, de végétation et d'influence humaine historique. L'activité anthropique actuelle diffère notablement entre les lacs. Elle est négligeable au Levi Pond et au North Round Pond, tandis qu'au bord de Bates Pond, quelques maisons sont présentes, et dans le lac Walden Pond des centaines de milliers de personnes se baignent chaque été à partir d'une plage et d'un site historique populaire. Cependant, les lacs possèdent une histoire semblable en ce qui concerne le déboisement et le rétablissement de la forêt dans le bassin versant. Ceci va permettre une interprétation des données provenant des derniers 1500 ans à l'échelle régionale. Le Table 1.1 décrit les caractéristiques principales des sites d'étude.

Table 1.1 Localisation, caractéristiques et dates d'échantillonnage des sites d'étude.

	Walden Pond	Bates Pond	North Round Pond	Levi Pond
État américain	Massachusetts	Connecticut	New Hampshire	Vermont
Longitude	71.3°W	72.0°W	72.5°W	72.2°W
Latitude	42.4°N	41.7°N	42.8°N	44.2°N
Altitude	50 m	95 m	317 m	497 m
Superficie du lac	25 ha	2.7 ha	5.26 ha	9.1 ha
Superficie du bassin versant	38 ha	68.2 ha	24.1 ha	57 ha
Profondeur maximale	30 m	3.6 m	3.4 m	3.2 m
pH	7.6	6.0	6.1	5.5
Niveau trophique	eutrophe	mésotrophe	mésotrophe	oligotrophe
Date de carottage	24 Fév. 2000	25 Mai 2000	20 Fév. 1997	11 Nov. 1994
Date de colonisation	1630 AD	1700 AD	1733 AD	1789 AD

1.7.2 Les études paléolimnologiques

Les études paléolimnologiques fournissent les informations sur l'état et la variabilité des écosystèmes lacustres et leur environnement dans le passé à partir des informations physiques, chimiques et biologiques conservées dans les sédiments lacustres (Pennington 1981; Battarbee et al. 2001; Bennett et Willis 2001; Walker 2001; Wolfe et al. 2001). Elles sont donc l'outil idéal pour l'étude des impacts du climat et de l'homme sur les écosystèmes lacustres dans le passé, surtout pour les régions et les périodes pour lesquelles aucun enregistrement historique est disponible. Relativement à nos objectifs, l'étude des sédiments datant d'avant l'arrivée des Européens va nous permettre d'estimer la variabilité naturelle des lacs. L'analyse des sédiments qui correspondent aux périodes où la qualité de l'eau n'a pas encore fait objet d'un suivi régulier nous permettra d'évaluer l'impact de l'activité humaine en combinaison avec l'influence du climat et d'étudier la façon dont les lacs ont réagi à la réinstallation de la végétation dans le bassin versant. Pour ce faire, dans chaque site de notre étude, une carotte de sédiments a été prélevée. Elles ont ensuite été sous-échantillonnées à un intervalle de 1 cm afin d'obtenir des échantillons à haute résolution temporelle pour les analyses multiples.

1.7.3 Les diatomées

Pour la présente étude, les diatomées (classe : Bacillariophyceae) ont été extraites des sédiments et analysées. Elles représentent un groupe d'algues unicellulaires qui se distinguent par une coquille siliceuse (frustule) finement ornementée qui est souvent bien préservée dans les sédiments des lacs. Leur forte abondance dans presque tous les environnements aquatiques, leur grand nombre d'espèces, la diversité de leurs préférences écologiques et la rapidité de leur réponse aux changements du milieu les rendent éminemment utiles pour l'indication quantitative des caractéristiques environnementales récentes et du passé (Dixit et al. 1992; Moser et al. 1996).

Les préférences écologiques et la distribution des diatomées le long des gradients environnementaux actuels peuvent être utilisées pour développer des modèles de reconstitution des conditions limnologiques, entre autres pour le niveau trophique (Bennion et al. 1996; Hall et Smol 1999), la salinité (Laird et al. 1998), le pH (Smol et al. 1986; Birks et al. 1990; Weckström et al. 1997), l'alcalinité (Davis et al. 1994b; Fallu et al. 2002), le COD (Kingston et Birks 1990; Pienitz et Smol 1993; Fallu et Pienitz 1999) et la température (Pienitz et al. 1995; Weckström et al. 1997; Joynt et Wolfe 2001). En appliquant ces modèles d'inférence sur les assemblages fossiles, les données obtenues peuvent servir d'une part à l'interprétation des dynamiques dans le bassin versant, tels que les changements de la végétation (Hall et Smol 1993; Pienitz et al. 1999) et les activités humaines (Harris et Vollenweider 1982; Stoermer et al. 1991; Wessels et al. 1999; Bennion et al. 2001; Francis et Foster 2001; Ramstack et al. 2003). D'autre part, on peut reconstituer les conditions climatiques, telle la température, de façon directe (Korhola et al. 2002; Bigler et Hall 2003; Wolfe 2003), où de façon indirecte par la dimension et la durée de la couverture de glace hivernale (Smol 1988; Edlund et al. 1995). L'humidité (ratio évaporation - précipitation) peut être reconstituée soit à partir de la salinité (Fritz et al. 2000) ou selon les changements du niveau lacustre indiqués par le ratio des espèces périphytiques/planctoniques (Gasse et al. 1989; Haworth 1993).

Dans notre étude, nous allons nous servir des diatomées en tant qu'indicatrices du pH, du niveau trophique de l'eau (par le biais de la concentration en phosphore total), du COD ainsi que de la disponibilité de l'habitat. Les changements du pH peuvent indiquer le contenu en ions provenant de l'activité humaine, refléter des changements végétaux ou indiquer le degré d'acidification par les émissions industrielles. Le niveau trophique est un indicateur standard de la perturbation anthropique. Pendant que l'usage des diatomées en tant qu'indicatrices de l'influence humaine est effectué dans toutes les régions, la majorité des études paléoclimatiques mentionnées ci-haut a été effectuée dans les régions arctiques ou sub-arctiques. Dans les régions tempérées, les diatomées sont plutôt contrôlées par la disponibilité des nutriments et par le pH. Elles répondent donc aux changements climatiques de façon plus subtile, tel que par des changements dans la dynamique saisonnière dus à la modification de la durée de mélange totale d'eau qui est étroitement associé au régime thermique (Bradbury et Dieterich-Rurup 1993; Edlund et al. 1995). En étudiant la dynamique saisonnière actuelle dans un lac, nous essayons de reconstituer les variation dans la répartition saisonnière des diatomées dans le passé. Puisque les concentrations en carbone organique dissous reflètent en grande partie les modifications dans la végétation du bassin versant, le développement des tourbières en périphérie du lac et l'humidité dans le bassin versant, elles serviront d'outil paléoécologique et paléoclimatique supplémentaire.

1.7.4 Analyses statistiques

Les reconstitutions quantitatives des paramètres limnologiques, tel que mentionné ci-dessus, sont devenues possibles grâce au développement des techniques statistiques multivariées. La reconstitution quantitative consiste en deux étapes d'analyse des données. D'abord, les assemblages de diatomées dans les sédiments de surface sont mises en relation avec les mesures chimiques et physiques de l'eau de plusieurs lacs (environ 30 à 60) d'une certaine région. Ces analyses statistiques permettent d'identifier les variables qui exercent la plus grande influence sur la répartition des populations diatomifères et pour lesquelles des fonctions de transfert (aussi appelés modèles d'inférence) peuvent être développées. La deuxième étape consiste en l'application de ces fonctions de transfert aux assemblages obtenus à partir des carottes de sédiment, ce qui permet d'estimer les valeurs d'une variable donnée pour une certaine période dans le passé. Puisqu'une différence considérable entre la composition des communautés du modèle et les assemblages des échantillons anciens peut falsifier les résultats, le dégrée d'analogie entre les assemblages fossiles et actuels est estimé pour évaluer la fiabilité des reconstitutions. Nous utilisons ici une partie d'un ensemble de données de diatomées de sédiment de surface et des variables physico-chimiques qui a été fourni par Dixit et al. (1999).

L'implication de plusieurs indicateurs dans une étude paléoécologique permet d'obtenir plus d'information qu'une simple confirmation répétée des résultats (Smol 1990). Chaque méthode a ses forces et ses faiblesses, donc leur combinaison rend les interprétations plus complètes. Le développement d'indicateurs différents, tel que les diatomées, les chrysophycées et les chironomides, rend les reconstitutions plus robustes car ils renforcent et amplifient les conclusions (Brugam, 1978). Pour notre étude cet aspect est particulièrement important dans l'effort de distinguer les facteurs climatiques des facteurs anthropiques. À partir de l'analyse des diatomées, l'influence humaine est facilement identifiable dans les sédiments, mais les changements climatiques sont plus difficilement enregistrés, tel que discuté ci-haut. Parmi les indicateurs paléolimnologiques analysés par les chercheurs-collaborateurs de ce projet, l'analyse de pollen permet de reconstituer les changements de la végétation qui peuvent refléter des variances climatiques ou l'activité humaine. Les larves de chironomides, qui sont des moucherons inoffensifs, servent à la reconstitution de la température de l'eau, donc du climat, et de la trophie qui est reliée à l'influence humaine. L chronologie des carottes de sédiment a été établie à partir de datations au ^{14}C et au ^{210}Pb. La consultation des documents historiques aide à identifier les changements biologiques des indicateurs qui sont dus à l'activité humaine et fournit de l'information sur la nature et l'intensité des activités anthropiques dans les bassins versants des lacs. L'analyse des isotopes stables de carbone, azote et oxygène contribue aux informations paléoclimatiques et paléohydrologiques.

Les pièges à sédiment sont utilisés afin d'obtenir de l'information sur la dynamique temporelle des populations de diatomées. Le principe de cette méthode est basé sur le fait qu'un flux des particules (p.e., organismes planctoniques, détritus) vers le fond du lac se produit constamment. En utilisant des dispositifs cylindriques (Bloesch et Burns 1980; Horn et Horn 1990), une portion de ces matériaux peut être échantillonnée pour déterminer la biomasse, la composition des espèces, le taux de sédimentation et les changements floristiques pendant une période de temps spécifique.

1.8 Contenu des chapitres

Les travaux et résultats de mon étude sont présentés dans les cinq chapitres suivants dont le contenu principal est détaillé ci-dessous.

Dans le deuxième chapitre, différents modèles d'inférence sont développés et leur performance est testée. Nous comparons les modèles basés sur les moyennes pondérées (weighted averaging), les moyennes pondérées avec la diminution du poids des tolérances (weighted averaging with tolerance-downweighting), les moyennes pondérées des moindres carrés partiels (weighted averaging partial least squares), les réseaux neuronaux artificiels (artificial neural networks) et la régression logit de Gauss (Gaussian logit regression) avec et sans transformation logarithmique des gradients environnementaux ainsi qu'avec et sans transformation de la racine carré des données biologiques. Les reconstitutions quantitatives résultant de l'application de ces modèles sur la carotte de Walden Pond, Massachusetts, sont comparées aux mesures de la chimie de l'eau dans ce site. Les résultats sont discutés en considérant le type de réponse des espèces vis-à-vis des variables environnementales.

Le troisième chapitre comprend la reconstitution paléoenvironnementale des derniers ca. 1500 ans pour Walden Pond, Massachusetts, par les diatomées et les isotopes stables. Le lac étant d'une grande valeur publique et historique par son importance dans l'œuvre du philosophe Henry David Thoreau, ce site a récemment connu des problèmes de qualité de l'eau. Notre étude évalue l'impact de la présence massive des touristes autour du lac par la reconstitution quantitative du phosphore total et du pH et par la composition isotopique, détermine le statut naturel du lac et évalue l'efficacité des mesures de gestion effectuées jusqu'à présent.

L'histoire environnementale de deux lacs, un au Vermont et l'autre au New Hampshire, en considérant l'influence humaine et climatique, est le sujet d'étude du quatrième chapitre. Par le biais du pH, TP et COD reconstitués, les effets du déboisement par les colons et la récupération des lacs après la réinstallation de la végétation sont évalués. De plus, la reconstitution du COD sert à vérifier si un changement de l'humidité régionale a affecté l'écosystème lacustre pendant la période étudiée.

Dans le cinquième chapitre, j'étudie les paramètres qui contrôlent la succession saisonnière des diatomées dans Bates Pond, au Connecticut, et j'applique ces résultats à l'interprétation des assemblages fossiles provenant la carotte sédimentaire du même lac. Deuxièmement, les périodes de productivité des diatomées le plus élevée sont identifiées afin de déterminer le moment le plus approprié de l'année pour la collecte des mesures limnologiques pour le développement d'un modèle de reconstitution.

Dans le sixième chapitre, les résultats obtenus dans les quatre lacs à l'étude sont résumés et comparés en tenant compte des résultats des autres indicateurs paléoécologiques fournis par les chercheurs-collaborateurs du même projet. En comparant les changements dans les différents indicateurs, et en estimant leur correspondance et leurs écarts temporels, j'essaie de développer une synthèse des facteurs régionaux et locaux qui ont contrôlé la dynamique des lacs et de leurs bassins versants pendant les derniers environ 1500 ans en Nouvelle-Angleterre.

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2 Diatom-based inference models and reconstructions revisited : methods and transformations

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2.1 Résumé

Différentes méthodes pour la reconstitution des variables environnementales à l'aide des diatomées ont été testées sur les données provenant de 82 lacs de la Nouvelle-Angleterre et des données d'une carotte de Walden Pond (Massachusetts, États-Unis). La méthode des moyennes pondérées et la méthode de la probabilité maximale ont reconstitué les valeurs des variables du gradient principal pH et alcalinité le plus près des valeurs mesurées à Walden Pond, tandis que les réseaux neuronaux artificiels et la méthode de la probabilité maximale ont mieux reconstitué la variable du gradient secondaire phosphore total. Les transformations des données ont eu divers effets sur les différents modèles car elles ont affecté de façon distincte le modèle de réponse des espèces envers les variables. Cette première application des réseaux neuronaux artificiels sur les diatomées fossiles a montré que cette méthode peut être supérieure pour reconstituer une variable du gradient secondaire, tandis que les méthodes classiques sont adéquates pour les gradients principaux.

2.2 Abstract

Different calibration methods and different data manipulations are commonly employed for quantitative paleoenvironmental reconstructions, but are rarely compared using the same data. Here, we compare several diatom-based models (weighted averaging (WA), weighted averaging with tolerance-downweighting (WAT), weighted averaging partial least squares

(WA-PLS), artificial neural networks (ANN) and Gaussian logit regression (GLR)) in different situations of data manipulation. We tested whether log transformation of environmental gradients and square-root transformation of species data improved the predictive abilities and the reconstruction capabilities of the different calibration methods and discussed them in regard to species response models along environmental gradients. Using a calibration data set from New England, we showed that all methods adequately modelled the variables pH, alkalinity and total phosphorus, as indicated by similar root mean square errors of prediction (RMSEP). However, WAT had lower performance statistics than simple WA and showed some unusual values in reconstruction, but setting a minimum tolerance for the modern species, such as available in the new computer program C^2 version 1.4, resolved these problems. Validation with the instrumental record from Walden Pond (Massachusetts, USA) showed that WA and WAT reconstructed most closely pH and that GLR reconstructions showed the best agreement with measured alkalinity, whereas ANN and GLR models were superior in reconstructing the secondary gradient variable total phosphorus (TP). Log transformation of environmental gradients improved model performance for alkalinity, but not much for TP. While square-root transformation of species data improved the performance of the ANN models, they did not affect the WA models. Untransformed species data resulted in better accordance of the TP inferences with the instrumental record using WA, indicating that, in some cases, ecological information encoded in the modern and fossil species data might be lost by square-root transformation. Thus it may be useful to consider different species data transformations for different environmental reconstructions. This study showed that the tested methods are equally suitable for the reconstruction of parameters that mainly control the diatom assemblages, but that ANN and GLR may be superior in modelling a secondary gradient variable. For example, ANN and GLR may be advantageous for modelling lake nutrient levels in North America, where there is a small range in TP concentrations.

2.3 Introduction

Quantitative reconstructions of past environments using freshwater and marine sediment records have become increasingly accepted over the last decades (Birks 1998). Inference models based on modern relationships between biota (such as diatoms) and the environment (pH, temperature, total phosphorus, etc.) are routinely applied to fossil biological data in order to infer quantitative environmental values for periods without adequate instrumental data coverage (Kauppila et al. 2002; Ramstack et al. 2003; Siver et al. 2003). In an attempt to obtain the potentially most reliable reconstructions, it is beneficial to compare reconstructed values based on different methods and to assess critical issues of the methodology employed (e.g., data screening, data transformations) (Birks 1998). However, in light of the large number of existing models, such considerations have only rarely been addressed (Korsman and Birks 1996; Hall et al. 1997).

Recently, artificial neural networks (ANNs) have been introduced to paleolimnological research and show promising performance when modelling pH with diatoms (Racca et al. 2001). However, the outputs of ANN models have not yet been comprehensively compared to the outputs of standard approaches (e.g., weighted averaging regression and calibration (WA) (ter Braak and van Dam 1989); weighted averaging partial least squares regression (WA-PLS) (ter Braak and Juggins 1993)) in the application to fossil diatom data, by validation with instrumental data and through the use of other variables than pH. This paper is an attempt to fill this gap by comparing diatom-based reconstructions using common methods (Gaussian logit regression (GLR), WA with classical deshrinking ($WA_{class.}$), WA with inverse deshrinking ($WA_{inv.}$), WA with tolerance-downweighting (WAT), and WA-PLS) with estimates obtained by ANNs and with instrumental records for Walden Pond, Massachusetts.

2.4 Data

2.4.1 Training set

The water chemistry and modern surface sediment diatom data used to develop diatom-based inference models originate from the United States Environmental Monitoring and Assessment Program – Surface Waters (EMAP-SW, data available via internet:

http://diatom.acnatsci.org/dpdc). In the northeastern United States (Maine, New Hampshire, Vermont, Massachusetts, Connecticut, New York, Rhode Island and New Jersey), 257 lakes were sampled during July and August 1991-1994. Details concerning sampling procedures and diatom sample processing are given in Dixit et al. (1999). A subset of 82 lakes was selected for model development and environmental reconstructions in lakes from Vermont, New Hampshire, Massachusetts and Connecticut (Fig. 2.1; Köster et al. Chapters 3, 4, and 5). The sites from Maine, New York, Rhode Island and New Jersey were excluded a priori in order to limit the calibration set to the geographical region where the lakes for paleolimnological studies are located. Model and reconstruction comparisons presented here are based on this smaller data set. The main characteristics of the data set are presented in Table 2.1 and the relation of the 82 surface diatom assemblages to major environmental variables and lake characteristics are illustrated in the ordination biplot resulting from a canonical correspondence analysis (CCA; Fig. 2.2).

2.4.2 Fossil data and analogs with training set

For reconstruction purposes, we used fossil diatom data from a 140 cm-long surface sediment core of Walden Pond (42°26.3'N, 71°20.4'W), spanning ca. 1600 years (Köster et al. Chapter 3). The ecological interpretation of the fossil diatom assemblages, the sedimentary stable isotope record, as well as the instrumental data of Walden Pond indicate a clear, albeit seasonal change in the lake water chemistry to higher nutrient concentrations during the 20th century (starting at about 10 cm depth; Köster et al. Chapter 3). This change is evident in the ordination of the fossil percentage data in a principal components analysis (PCA), with inter-sample distance scaling and covariance matrix (Fig. 2.3).

Table 2.1 Major characteristics of the diatom and environmental data of the training set. Ordination results are given for the 189-species set (cut-off-criterion: 1 occurrence at 1%).

No. of samples		82
No. of species	total	371
	1 occurrence at 1%	189
	min. 10 occurrences	121
species DCA	lambda	7.2
CCA axis 1	% variance	8.4
CCA axis 2	% variance	4.1
pH	min	4.99
	max	8.6
	mean	7.5
	median	7.6
	length of gradient in DCCA	4.0
	% variance in CCA	6.0 (p=0.005)
alkalinity	min	-9.5
	max	1858
	mean	399
	median	201.5
	length of gradient in DCCA	4.5
	% variance in CCA	6.1 (p=0.005)
TP	min	0.85
	max	109.5
	mean	16.1
	median	11
	length of gradient in DCCA	2.6
	% variance in CCA	3.4 (p=0.005)

DCA = detrended correspondence analysis. CCA axes 1 and 2 = first two axes in a canonical correspondence analysis with 17 environmental variables (see also Fig. 2.2). CCA = CCA constrained to one variable. DCCA = detrended canonical correspondence analysis. % variance = percentage of variance in species data which is explained by this axis or variable.

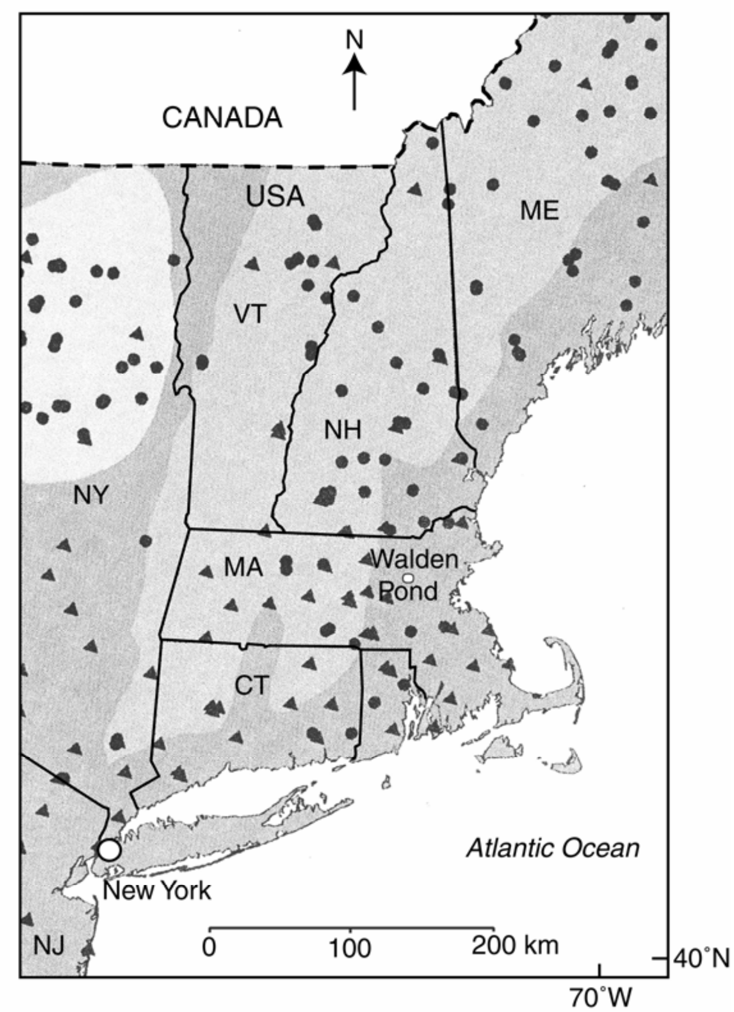

Figure 1 Map of the training set sites in the New England states Vermont (VT), New Hampshire (NH), Massachusetts (MA), and Connecticut (CT) and location of the study site Walden Pond.
ME = Maine. NY = New York. NJ = New Jersey. grey areas: New England Uplands. dark grey areas: Coastal Lowlands/Plateau. light grey area = Adirondacks. Modified from Dixit et al. (1999).

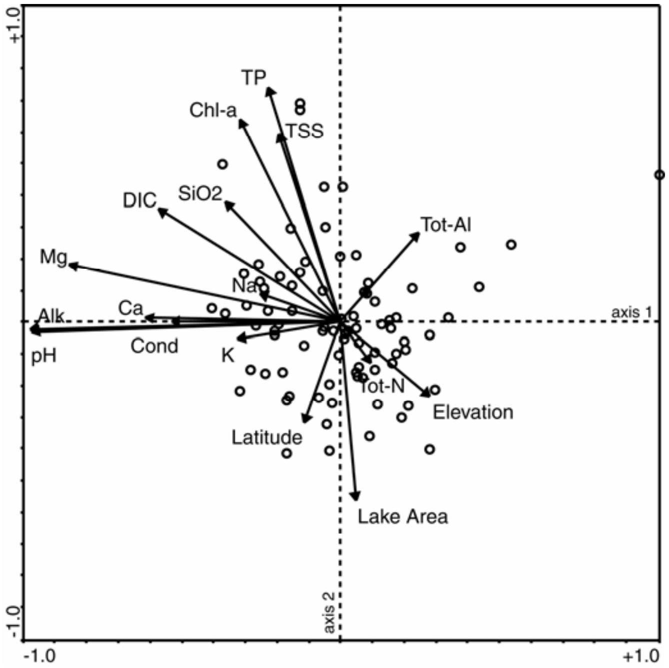

Figure 2 Environmental variables/sample biplot derived from CCA including subfossil diatom data from 82 New England sites and corresponding lake water measurements.
TP = total phosphorus, TSS = turbidity , Chl-a = chlorophyll *a*, SiO_2 = silica, DIC = dissolved inorganic carbon, Mg = magnesium, Na = sodium, Ca = calcium, alk = alkalinity, Cond = conductivity, K = potassium, Tot-N = total nitrogen, Tot-Al = total aluminium.

The analogs of the fossil samples with the training set were estimated by means of dissimilarity coefficients using chord distance (Overpeck et al. 1985), where fossil samples inside the 75% confidence interval of the mean minimum dissimilarity coefficient of the training set samples have good analogs, samples outside the 75% and inside the 95% confidence interval have poor analogs, and samples outside the 95% limit have no analogs (Laing et al. 1999). Fit of the fossil samples to the environmental gradient in the training set was estimated by CCA constrained to pH and TP as the single explanatory variables. Fossil samples with a residual distance inside the 90% confidence interval of the residual distances of the modern samples to the first CCA axis have a good fit, and samples outside the 90% limit have poor fit (Birks et al. 1990).

Analog and goodness-of-fit analyses of modern and fossil samples distinguished two different groups of core samples (Köster et al. Chapter 3). Samples between 140 cm and 9 cm had good analogs and good fits, indicating that the fossil diatom flora is well represented in the modern training set. With the exception of levels 4, 3 and 0 cm, the samples from 8 to 0 cm had poor analogs, and all levels from 8 to 0 cm had poor fit to both pH and TP. The poor analogs in the upper 8 cm were caused by very high abundances of three species, which are present at lower abundances in the calibration set (e.g. *Asterionella formosa* Hassal, *Tabellaria flocculosa* (Roth) Kütz. str. IIIp sensu Koppen, *Fragilaria nanana* Lange-Bertalot, likely synonymous with *Synedra delicatissima* W. Smith in the training set). These species show a significant unimodal response to pH in the training set (Köster et al. unpublished data), indicating that useful parameters were estimated for the pH model. However, only *Synedra delicatissima* and *Tabellaria flocculosa* str. IIIp show a unimodal response to TP, in contrast to *Asterionella formosa* with no significant response to TP. This may have resulted in less reliable TP-model parameters for *A. formosa*. In summary, the analog analyses indicate that the reconstructions from 140 to 9 cm are reliable for pH and TP, and that the reconstructions from 8 to 0 cm are reliable for pH and probably not precise for TP. Analog analyses with alkalinity were not carried out, but as alkalinity is closely correlated with pH, it is likely to behave similarly.

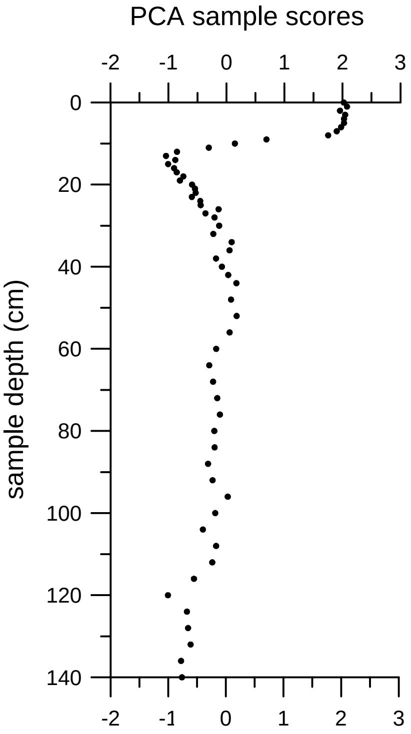

Figure 3 PCA scores of fossil diatom samples from Walden Pond sediments.

2.4.3 Instrumental record of Walden Pond

Limnological surveys of the study site (Baystate Environmental Consultants 1995; Colman and Friesz 2001) provide instrumental data for validation of the diatom-inferred values (Table 2.2). As the records are not continuous and were established by different investigators, some details regarding the variables of interest are detailed below.

The pH of Walden Pond can change significantly during the course of one year (Table 2.2), particularly in the euphotic zone, where planktonic algal growth takes place and photosynthetic CO_2 depletion leads to pH values up to 9. The arithmetic mean pH of 7.8 for the years 1997 and 1999 is based on 129 and 111 measurements, respectively, dating from all months and integrating several depths of the epilimnion (0-15 m, in 1 m-steps). pH measurements before 1990 were taken after transport of the water to the laboratory (Arthur Johnson, Massachusetts Department of Environmental Protection, personal communication), which may affect significantly the pH of the samples. Therefore we use only the pH data based on standard, in situ methods for validation of the diatom-inferred pH values.

Total phosphorus concentrations were below the detection limit of 10 $\mu g\ l^{-1}$ during much of the year, but peaked in summer when intensive recreational use caused significant external nutrient loading to the lake (Baystate Environmental Consultants 1995). Therefore, mean annual data for TP camouflage the nutrient enrichment over the summer months that strongly affects the diatom assemblages (Köster et al. Chapter 3).

In contrast to pH and TP, alkalinity was more stable throughout the year and thus easier to compare with diatom-inferred values.

Table 2.2 Instrumental record for pH, alkalinity, and total phosphorus in Walden Pond, measured on epilimnetic water (Baystate Environmental Consultants 1995; Colman and Friesz 2001).

	1986	1989	1994	1997	1999
pH					
median	n.d.	n.d.	n.d.	7.9	7.6
average	n.d.	n.d.	n.d.	7.8	7.6
min	n.d.	n.d.	n.d.	6.4	6.4
max	n.d.	n.d.	n.d.	9.4	9.4
number of samples	n.d.	n.d.	n.d.	129	111
total phosphorus (µg l^{-1})					
median	n.d.	40	10	8.4	6.5
average	n.d.	57.5	<16,7	8.6	6.7
min	n.d.	10	<10	2.5	4.5
max	n.d.	140	60	19.5	8.7
number of samples	n.d.	8	12	38	7
alkalinity (µeq l^{-1})					
median	259	220	152	n.d.	n.d.
average	269	225	155	n.d.	n.d.
min	214	220	134	n.d.	n.d.
max	340	240	182	n.d.	n.d.
number of samples	6	8	12	n.d.	n.d.

Values preceded by a less than sign (<) indicate measurements below detection limit. n.d. = no data.

2.5 Methods

Detrended correspondence analysis (DCA) on the raw species data indicated high variation in diatom assemblages with a total variance of 7.2 (Table 2.1). Therefore, methods assuming unimodal species responses to the environmental gradients, such as canonical correspondence analysis (CCA), can be applied (Birks 1995). As the distributions of alkalinity and total phosphorus data were skewed, they were normalized by $\log_{10}$-transformation. Models based on non-transformed environmental data were developed for comparative purposes.

Diatom inference models were developed for the variables pH, alkalinity (alk) and TP, as they explained most of the variation in the surface diatom data, as indicated by CCA (Fig. 2.2, Table 2.1). DCCA (detrended canonical correspondence analysis) with each individual variable as a predictor and detrending by segments and non-linear scaling indicated gradient lengths of larger than 2 standard deviations (SD) for all three variables (pH: 4.0, alk: 4.5, TP: 2.6), indicating that methods dealing with unimodal species responses are appropriate for model development. Although alkalinity and pH were highly correlated, we included models and reconstructions for both parameters. The performances of the models were compared by means of the determination coefficient (r^2), root mean square error of prediction (RMSEP), the mean and maximum bias as well as by the degree of coherence between the diatom-inferred values and the instrumental data. Bootstrapped performance statistics are presented, but comparisons between different methods are based on leave-one-out cross-validation (jackknifing), because it was the only available cross-validation method for ANN. Mean and maximum bias was calculated using the new approach presented by Racca and Prairie (2004).

The ordination techniques DCA, DCCA, CCA, and PCA were performed using the computer program CANOCO for Windows version 4.0. The computer program C^2 version 1.4 (Juggins 2003) was used to develop diatom-based inference models, to assess their performance, to reconstruct environmental variables and to calculate the sample-specific errors using bootstrapping. Aside from the common procedure for WAT, a new algorithm was used where small tolerances were replaced by a fraction (0.1) of the gradient. This strategy was developed in order to avoid the attribution of very high weight to rare species with small tolerances

(Steve Juggins, personal communication), which otherwise may lead to low performance estimates (Table 2.3) and erroneous reconstructions (Fig. 2.4c).

The models based on artificial neural networks were implemented using YANNS (Yet Another Neural Network Simulator; Boné et al. 1998). Principles underlying this method are described in detail by Racca et al. (2001). For modelling alkalinity with ANN, one extreme site was removed, because the difference between the measured and the predicted value (residual) of this site was three times greater than the mean residual of all other sites.

The distribution of species over the environmental gradients was determined by testing a hierarchical set of response models (Huisman et al. 1993), implemented in the program HOF (Oksanen and Minchin 2002). For each species, HOF is returning the simplest of five possible models (skewed (= asymmetric) unimodal, symmetric unimodal, sigmoidal (increasing or decreasing), plateau, no trend), which does not result in a statistically significant rise in the residual deviance. All species with at least 10 occurrences were selected for this analysis, which reduced the number of species included from 189 to 121. For percentage species data, a binomial error distribution was used in the program, whereas for square-root-transformed data, the Poisson distribution was chosen.

2.6 Results and discussion

2.6.1 Performance of different models

In general, the predictive abilities of the models for pH and alkalinity as reflected by r^2_{jack} were better than those of the TP models (Table 2.3), a common feature of training sets including a long pH gradient and a shorter TP gradient (Hall and Smol 1996; Dixit et al. 1999; Siver 1999). For pH and alkalinity, ANN resulted in the lowest RMSEP (0.23 - 0.25), followed by WA-PLS 2 and WAT with RMSEPs of 0.26 - 0.28 and WA (0.27 - 0.30). For modelling TP, WA-PLS 2 had slightly lower RMSEP (0.23) than WA_{class}, WA_{inv}, and ANN, which performed equally well with RMSEPs between 0.25 and 0.26. GLR had lower jackknifed performance, but better apparent performance than the WA methods for pH and alkalinity and lower apparent and bootstrapped performance for TP.

In contrast to WAT using a lower limit for species tolerances, such as applied here, WAT without this option, such as in the former version of C^2 and the programs WACALIB and CALIBRATE, performed less well by ca. 0.1 to 0.2 in RMSEP (Table 2.3). When rare taxa were excluded (Köster et al. unpublished data), the performance of tolerance-downweighted WA equalled that of the other WA methods. This confirms results of previous studies (Birks 1994; Wilson et al. 1996), which showed that the performance of WA with tolerance-downweighting decreases with inclusion of rare species. This may be explained by the difficulty of estimating a relatively realistic tolerance value for species with a low number of occurrences. In our training set, for example, a tolerance value of 0.1 and an optimum of 8.5 was calculated for *Fragilaria construens* var. *venter,* which does not make sense ecologically and led to low model performance (Table 2.3) and unusual reconstructions (Fig. 2.4c). The definition of a minimum tolerance for species in the training set, such as implemented in the recent version 1.4 of the computer program C^2 (Juggins 2003), resolved this problem. Alternatively, tolerance estimates for species that do not display unimodal distributions over the gradient may be incorrect. Such taxa were well represented in our models (44 % and 67 % for pH and TP, respectively; Table 2.4), percentages that are comparable to those reported for other diatom training sets (Lotter et al. 1998; Cameron et al. 1999). WA with tolerance-downweighting has often been discarded in model choice for transfer functions because of lower performance (e.g. Birks et al. 1990; Hall and Smol 1992; Siver 1999). However, our results indicate that WAT may be a good alternative to WA for future inference model developments, if rare species are deleted or minimum tolerances are defined.

Table 2.3 (next page) Performance statistics for different models.
Alk = alkalinity. TP = total phosphorus. WA class. = Weighted averaging with classical deshrinking. WAT inv. = WA with inverse deshrinking and with tolerance-downweighting. WAT* inv. = WAT inv. computed with small tolerances replaced by a fraction of the gradient (0.1), see method section for details. WA inv. = WA with inverse deshrinking. WA-PLS 2 = WA partial least squares, two-component model. ANN = artificial neural networks. GLR = Gaussian logit regression (maximum likelihood). r^2 = apparent coefficient of determination of the regression of the predicted on the observed values. RMSE = apparent root mean square error of prediction. r^2 jack = jackknifed r^2. r^2 boot = bootstrapped r^2. RMSEP jack = jackknifed RMSE. RMSEP boot = bootstrapped RMSE. RMSEP back-trans = back-transformed RMSEP boot. Mean bias = average of residuals. Max. bias = maximum bias. Grey-shaded lines indicate the models with the best jackknifed performance for each variable.

variable	method	sites	environmental data transformation	species data transformation	r^2	RMSE	r^2 jack	RMSEP jack	r^2 boot	RMSEP boot	RMSEP back-trans	mean bias jack	max. bias jack
pH	WA class.	82	-	square root	0.85	0.28	0.81	0.30	0.80	0.31	-	-0.01	0.69
	WA inv.	82	-	square root	0.85	0.26	0.81	0.30	0.80	0.32	-	-0.01	0.89
	WAT inv.	82	-	square root	0.81	0.29	0.65	0.40	0.75	0.43	-	0	1.29
	WAT inv.*	82	-	square root	0.87	0.24	0.83	0.28	0.83	0.32	-	0	0.85
	WA inv.	82	-	-	0.87	0.24	0.82	0.29	0.81	0.33	-	-0.01	0.57
	WA-PLS 2	82	-	square root	0.94	0.16	0.83	0.28	0.82	0.31	-	0.01	0.94
	GLR	82	-	-	0.88	0.24	0.79	0.31	0.74	0.38	-	-0.01	0.76
	ANN	82	-	-	0.93	0.18	0.77	0.34	-	-	-	-0.06	-0.65
	ANN	82	-	square root	0.99	0.08	0.86	0.25	-	-	-	-0.01	0.86
Alk	WA class.	82	$\log_{10}(x+10)$	square root	0.86	0.23	0.80	0.27	0.80	0.28	1.88	-0.01	1.08
	WA inv.	82	$\log_{10}(x+10)$	square root	0.86	0.22	0.80	0.27	0.79	0.28	1.92	-0.01	1.30
	WAT inv.	82	$\log_{10}(x+10)$	square root	0.75	0.29	0.47	0.45	0.75	0.38	2.41	0.04	1.66
	WAT inv. *	82	$\log_{10}(x+10)$	square root	0.87	0.21	0.82	0.25	0.82	0.28	1.90	0	0.74
	WA-PLS 2	82	$\log_{10}(x+10)$	square root	0.95	0.13	0.80	0.26	0.81	0.28	1.89	0.01	1.45
	WA inv.	82	$\log_{10}(x+10)$	-	0.88	0.20	0.81	0.26	0.81	0.29	1.95	0	1.08
	WA inv.	82	-	-	0.76	240	0.63	301	0.62	327	-	127	-533
	WA inv.	82	-	square root	0.82	211	0.73	256	0.72	282	-	129	-487
	GLR	82	$\log_{10}(x+10)$	-	0.90	0.19	0.75	0.29	0.71	0.34	0.00	-0.01	1.43
	ANN	81	$\log_{10}(x+10)$	-	0.94	0.15	0.78	0.28	-	-	1.91	-0.05	0.82
	ANN	81	$\log_{10}(x+10)$	square root	0.96	0.11	0.85	0.23	-	-	1.69	-0.04	1.38
TP	WA class.	82	$\log_{10}$	square root	0.70	0.22	0.45	0.26	0.43	0.27	1.86	-0.01	0.47
	WA inv.	82	$\log_{10}$	square root	0.70	0.18	0.44	0.25	0.42	0.27	1.84	-0.01	0.56
	WAT inv.	82	$\log_{10}$	square root	0.43	0.25	0.11	0.34	0.34	0.31	2.04	0.02	-0.75
	WAT inv.*	82	$\log_{10}$	square root	0.70	0.18	0.42	0.25	0.40	0.27	1.88	0	0.45
	WA-PLS 2	82	$\log_{10}$	square root	0.80	0.15	0.50	0.23	0.48	0.25	1.79	-0.01	0.53
	WA inv.	82	$\log_{10}$	-	0.47	0.20	0.37	0.26	0.35	0.28	1.89	-0.02	-0.54
	WA inv.	82	-	square root	0.81	8	0.41	14	0.39	15	-	-0.84	-54
	WA inv.	82	-	-	0.77	9	0.30	16	0.29	16	-	-1.41	-64
	GLR	82	$\log_{10}$	-	0.66	0.23	0.35	0.30	0.34	0.30	2.00	-0.05	0.39
	ANN	82	$\log_{10}$	-	0.66	0.20	0.33	0.27	-	-	1.86	0	0.56
	ANN	82	$\log_{10}$	square root	0.76	0.16	0.39	0.26	-	-	1.81	-0.01	-0.56

2.6.2 Transformation of species data

Square-root transformation of the species data did not considerably affect the performance of any WA model with decreases by 0.01 in RMSEP (Table 2.3). All WA models behaved similar in this regard for all variables, therefore only the results for WA_{inv} are presented as an example. For ANN models, it resulted in lower RMSEP by 0.05 and 0.09 for alkalinity and pH, respectively, but only by 0.01 for TP (Table 2.3). Therefore, we can conclude for our training set data that species transformation did not affect the performance of WA models, but improved the performance of some ANN models.

2.6.3 Transformation of environmental data

Powerful ANN models for alkalinity and TP were obtained when using log-transformed environmental data. As RMSEP and bias are given in untransformed units, comparison with log models is difficult. However, log transformation resulted in higher r^2_{jack} for all WA models, indicating much better performance for alkalinity (increase in r^2_{jack} by 0.07 - 0.18) and fairly better performance for TP (increase of r^2_{jack} by 0.03 – 0.07). When alkalinity data were log-transformed, the number of unimodal species responses to this variable increased by 29 and 21 for untransformed and square-root-transformed species data, respectively. This indicates that log transformation normalized the skewed raw alkalinity data, thereby helping to relate the presumed unimodal species distributions to alkalinity and thus improving model performance. After log transformation of TP, however, the number of significant unimodal responses declined from 40 to 32 for untransformed species data and from 22 to 20 for square-root transformed data (Table 2.4). In this case, log transformation did not help to relate species distributions to the phosphorus data and therefore did not improve greatly the performance of the TP models. As the diatoms in our data set responded primarily to pH/alkalinity and less to the secondary TP gradient, they were perhaps generally less likely to show significant responses to TP, whatever the data manipulation might have been.

2.6.4 Comparison of reconstructions produced by different models and validation with the instrumental record

The paleoenvironmental reconstructions for Walden Pond produced by different methods showed generally the same pattern for pH and alkalinity, and to some extent also for TP. Relatively stable values were obtained for the samples from 140 to 12 cm and a more or less pronounced increase is evident between 11 cm depth and the surface (0 cm) (Figs. 4-6). This change reflects the recent, major shift in fossil diatom assemblages as demonstrated by the PCA sample scores (Fig. 2.3). Nonetheless, in some cases the absolute diatom-inferred values differed between methods.

2.6.4.1 pH

All WA models and WA-PLS 2 produced very similar pH reconstructions, therefore we only present WA_{inv} and WAT_{inv} for model comparison (Fig. 2.4a). From 140 to ca. 10 cm, GLR and ANN reconstructed lower values than the WA models by ca. 0.4 units. From 8 to 0 cm, GLR values approximated the WA reconstructions, whereas ANN values remained lower by ca. 0.4 units. The methods that estimated most closely the measured data were $WA_{inv,}$ WAT_{inv} and GLR, despite the lower performance statistics of the GLR model.

Different species transformations caused some differences between the model outputs. Square-root transformation led to higher values by 0.3 units for WA_{inv} inferences (Fig. 2.4b), as well as to lower values by 0.4 units for ANN reconstructions in the samples from 11 to 0 cm (Fig. 2.4b), compared to reconstructions using percentage species data. However, the differences remained well within the overlapping bootstrapped error ranges of the methods (0.32 and 0.33 for WA_{inv}; 0.25 and 0.34 for ANN) indicating that the pH reconstructions are not significantly affected by different species data transformations.

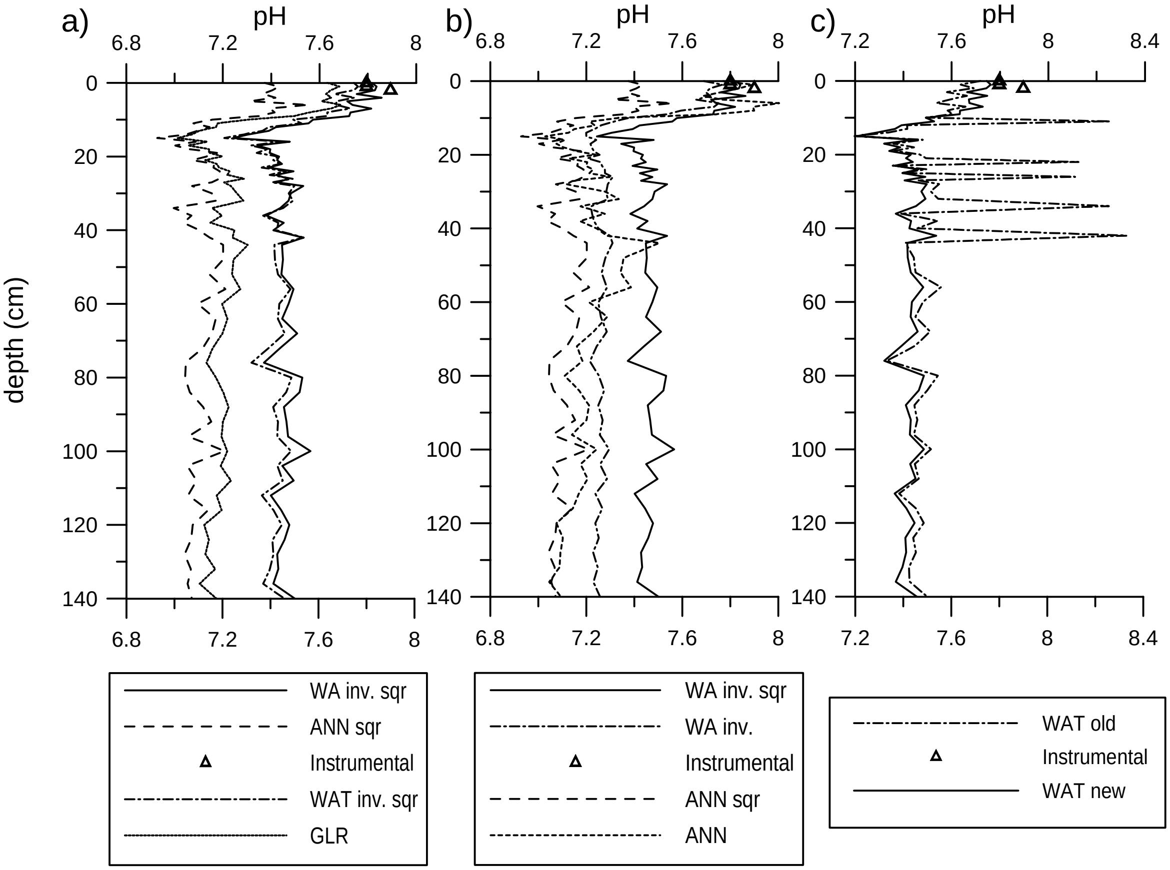

Figure 4 Comparison of diatom-inferred pH using different models.
For error values see text. a) different methods. b) different species transformations for WA inv. and ANN. c) weighted averaging with tolerance-downweighting (WAT). WAT old = WAT using the common algorithm. WAT new = WAT with minimum tolerance set to 0.1 of the gradient. WA inv. = weighted averaging with inverse deshrinking. WAT inv. = weighted averaging with tolerance-downweighting and inverse deshrinking. GLR = Gaussian logit regression (= maximum likelihood). ANN = artificial neural networks. instrumental = measured pH. sqr = square-root transformed species data

The differences between WAT-based reconstructions without defining a minimum tolerance (common method) and with tolerance limit (new method) are large in five samples, with deviations around 0.8 pH units (Fig. 2.4c). As all other methods reconstructed similar values to those generated by the new WAT method, without yielding abrupt pH changes in the past, the old method appears to produce unrealistic deviations in reconstructions. This problem is likely related to the unreliable tolerance estimates for rare species in the training set and can be avoided by defining a minimum tolerance, as discussed above (Steve Juggins, personal communication).

2.6.4.2 Alkalinity

Back-transformed diatom-inferred alkalinity values were comparable for all WA models (Fig. 2.5a). ANN and GLR reconstructed lower values by ca. 100 μeq l^{-1} from 140 to 9 cm. From 8 to 0 cm, GLR approximates the WA reconstructed values, whereas ANN values remained lower than the WA values by ca. 200 μeq l^{-1} (Fig. 2.5a). The difference seemed to be larger in recent sediments, with a maximum divergence in diatom-inferred alkalinity between the ANN and the WA_{inv} model of ca. 250 μeq l^{-1}, but the log-alkalinity values showed that the differences were equally large throughout the whole sediment sequence (Fig. 2.5b). The exponential function underlying the back-transformation of log values boosted the reconstructed values (and the associated prediction errors) in the upper levels and made them appear artificially high. Actually, the differences between the ANN and WA_{inv} reconstructions were within the overlapping errors of both inferences, which intersect by about 50-100 μeq l^{-1} (data not shown).

Each of the methods inferred closely one of the different measured alkalinity values, but over- or underestimated the other values, with one value outside the error limit of ANN and WA reconstructions, respectively. The coincidence of these deviations with poor analogs for the levels 8 to 0 cm suggests that the no-analog situation plays a role in the observed pattern.

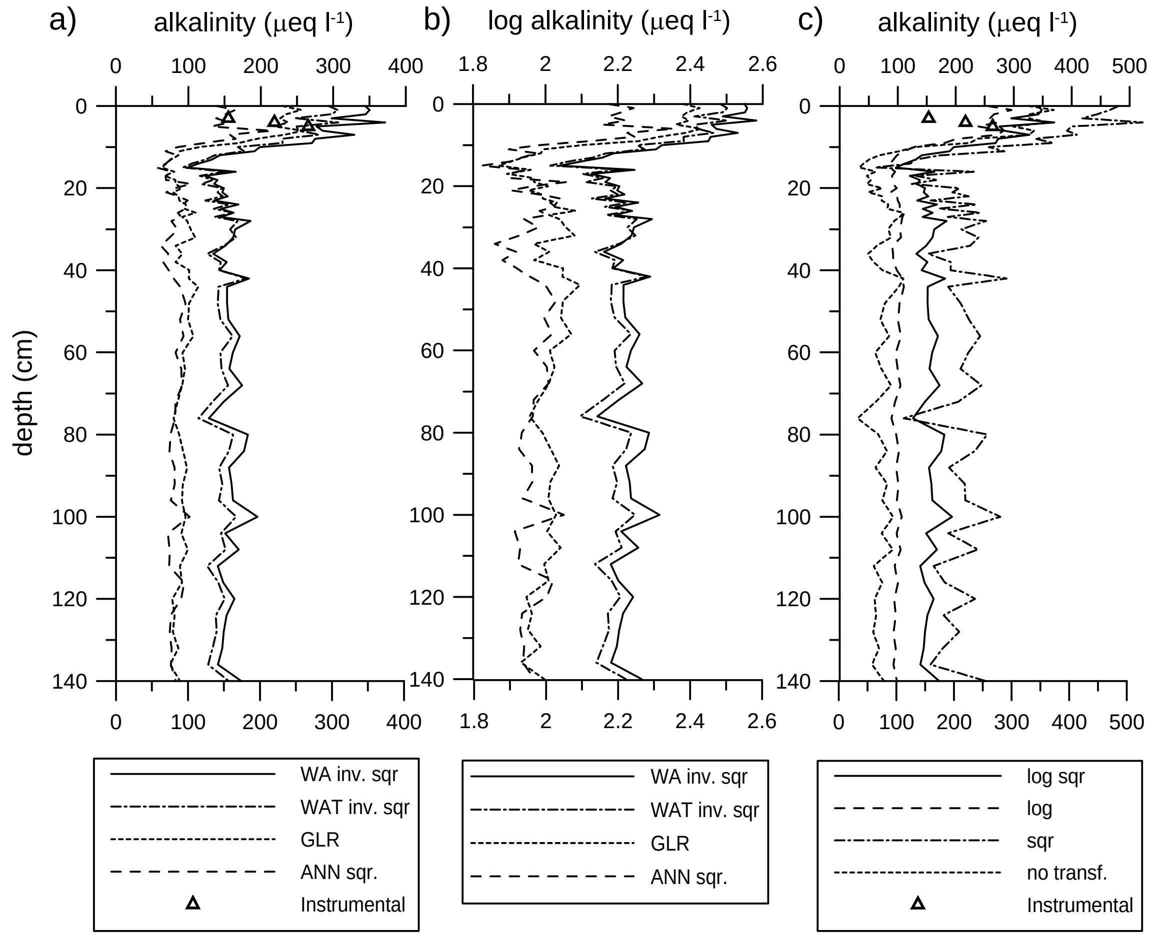

Figure 5 Comparison of diatom-inferred alkalinity using different models.
For error values see text. a) different methods. b) log alkalinity. c) different data transformations using WA inv.. WA inv. = weighted averaging with inverse deshrinking. WAT inv. = weighted averaging with tolerance-downweighting and inverse deshrinking. GLR = Gaussian logit regression (= maximum likelihood). ANN = artificial neural networks. Instrumental = measured alkalinity. log sqr = log alkalinity, square-root transformed species data. log = log alkalinity, untransformed species data. sqr = alkalinity, square-root transformed species data. no transf. = no data transformation.

When species, which are rare in the training set (here: *Asterionella formosa* and *Fragilaria nanana*), become a dominant part of the fossil assemblage, unusual reconstruction values can be the result. Classical methods are known to extrapolate better at the end of gradients (ter Braak 1995), a situation that may be present in the recent sediments of Walden Pond. However, in our example WA_{class} (data not shown) and WA_{inv} resulted in the same reconstructions, indicating that both methods dealt likewise with the no-analog situation. The only method that approximated each of the values sufficiently was GLR, despite its lower performance. In our case, GLR appears to provide a "mean" reconstruction between WA and ANN, which simulates a consensus reconstruction developed by combining results of different procedures, such as recommended by Birks (1995). The recent declining tendency in alkalinity was not evident in the reconstructions, perhaps indicating a delayed response of the diatoms to the change.

Different data transformations resulted in different alkalinity reconstructions from 140 to 10 cm, with the largest differences between models with and without square-root transformation (Fig. 2.5c). In the upper 8 cm, the reconstructions of the models converge, except of the model using untransformed alkalinity data and square-root transformation of species data, which exceeded by 100 to 170 $\mu eq\ l^{-1}$ the other inferences. The WA alkalinity models without species transformation produced similar reconstructions to those of ANN and GLR displayed in Fig. 2.5a, suggesting that WA models without species transformation approximated better the consensus reconstruction, as discussed above. Noticeably, the square-root transformation of species abundances, which normally should stabilize variances, resulted in higher intra-series variability, as indicated by higher standard deviations in the reconstructed data (33 versus 6 $\mu eq\ l^{-1}$ for the reconstructions from 140 to 10 cm for WA_{inv} sqr and WA_{inv}, respectively, note that this is also the case for pH and TP reconstructions). This may be a disadvantage when quantitative reconstructions are to be correlated with other independent proxy estimates.

2.6.4.3 Total Phosphorus

From 140 to 9 cm, all methods produced a similar, stable trend, but different values between ca. 3 $\mu g\ l^{-1}$ for GLR and ca. 7 $\mu g\ l^{-1}$ for WA and WAT (Fig. 2.6a). From 8 cm to 0 cm, ANN and GLR-inferred values increased by around 4 $\mu g\ l^{-1}$, whereas WA_{inv} and WAT-inferred values continued to fluctuate in the same range as in the other samples, with a slight trend to lower values. The weighted averaging methods resulted in more inter-sample variability than ANN and GLR throughout the core (Fig. 2.6a).

When different data transformations were applied in WA_{inv}, the reconstructed values differed by 3 $\mu g\ l^{-1}$ (Fig. 2.6b). Most reconstructions showed no trend, except of the log TP model without species transformation, which increased in the upper levels by 2 $\mu g\ l^{-1}$. The model with untransformed TP data and square-root-transformed species data resulted in negative values and is therefore not presented.

Almost all reconstructed TP values were smaller than 10 $\mu g\ l^{-1}$, corresponding well to the measured mean annual TP of 10 $\mu g\ l^{-1}$and less. The WA_{inv} model using untransformed species data, GLR and the ANN model tracked best the important assemblage change and higher seasonal TP maxima (Table 2.2) by inferring increasing TP values in the upper levels, although they had similar or lower statistical performance as the other WA models (Table 2.3). Similar results were obtained in some British Columbia lakes, where the best accordance of diatom-inferred TP with the instrumental record was achieved using untransformed species data in WA (Hall et al. 1997). In our case, this result is likely due to the fact that few species dominate the recent samples. Their high abundances helped detect a signal that was otherwise down-weighted by transformation. Another explanation may be found in the modern species response to TP. The untransformed TP and species data resulted in 40 significant skewed and symmetric unimodal distributions compared to about the half of that when square-root transformed diatom data were related to TP (22) and log TP (20) (Table 2.4). It appears that the square-root transformation of species data flattened unimodal species responses to TP to sigmoidal or non-significant ones, thereby removing information that may be useful for environmental inferences performed with this calibration set.

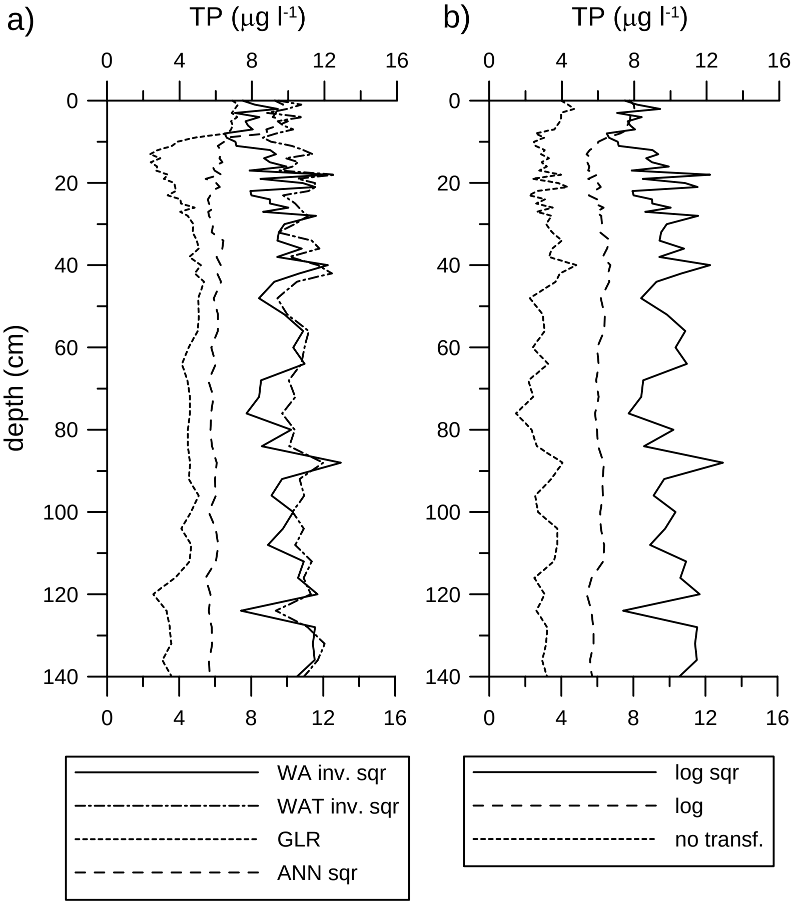

Figure 6 Comparison of diatom-inferred total phosphorus using different models. For error values see text. a) inferred total phosphorus produced by different methods. b) inferred total phosphorus using different data transformations. WA inv. = weighted averaging with inverse deshrinking. WAT inv. = weighted averaging with tolerance-downweighting and inverse deshrinking. GLR = Gaussian logit regression (= maximum likelihood). ANN = artificial neural networks. Instrumental = measured total phosphorus. log sqr = log total phosphorus, square-root transformed species data. log = log total phosphorus, untransformed species data. no transf. = no data transformation.

However, square-root transformation may have no effect at all in reconstructions using more diverse fossil assemblages with low abundances displayed by many species.

Reasons for the better correspondence between the ANN reconstructed TP values and the instrumental record may be that this method copes better than WA with poor-analog situations and/or high percentage of non-unimodal species responses. The latter is a known advantage of the ANN models (Racca et al. 2001). Therefore, this method may prove advantageous for modeling lake nutrient status in regions where the development of TP models using weighted averaging is challenging due to relatively small ranges in TP concentrations, such as in North America.

As the TP models had lower performance in comparison to the pH and alkalinity models, the TP reconstructions may be considered less reliable. Nonetheless, the comparison with the instrumental record showed that our models were suitable for the reconstruction of past total phosphorus concentrations. Also, reconstructions of TP for Lake Saint-Augustin in Québec using our TP model without species transformation showed good agreement with measured TP (K. Roberge, unpublished data).

2.7 Conclusions

The comparison of different methods in diatom-based reconstruction and validation by the instrumental record showed that weighted averaging with classical and inverse deshrinking as well as with and without tolerance-downweighting, Gaussian logit regression and artificial neural networks all provided reliable inference models and reconstructions for pH and alkalinity. In our study from Walden Pond, this was even the case under poor-analog conditions. However, using the common algorithm for WAT resulted in lower performance statistics than simple WA and in unusual reconstruction values, because rare species with small tolerances were highly weighted. Defining a minimum tolerance for the modern species, such as available in the new computer program C^2 version 1.4, resolved these problems. While WAT was often discarded for transfer function development in previous studies because of low performance, our results indicate that it may be an equally useful tool for paleoecological studies as simple WA.

Not all WA models for TP indicated the nutrient enrichment effect that was evident from changes in the phytoplankton community structure. The latter was inferred from the statistically equally well performing ANN and GLR models. These results suggest that the tested methods are equally suitable for the reconstruction of parameters that mainly control the diatom assemblages, but that ANN and GLR may be superior in modelling a secondary gradient variable. For example, ANN and GLR may be advantageous for modelling lake nutrient levels in North America, where TP gradients are relatively short.

Logarithmic transformation of skewed environmental data improved much the model performance of alkalinity, but only slightly the total phosphorus models. It appears that the primary response of diatom species to the main gradient inhibits the sensitivity of model performance to data manipulations regarding the secondary gradient.

Square-root transformation of species data did not improve the performance or the paleoecological inferences of the WA models, but was advantageous for the ANN models. Untransformed species data resulted in better accordance of the TP inferences with the instrumental record using WA, indicating that, in some cases, ecological information encoded in the modern and fossil species data might be lost by square-root transformation. In contrast to our expectations, square-root transformation of species data did not stabilize variances, but created more noisy reconstructions than models without square-root transformation. Thus it may be useful to consider different species data transformations for different environmental reconstructions.

Obviously, these conclusions cannot be generalized as they are only based on tests using one modern and one fossil data set. Future work on other fossil sequences from the same region will assess if diatom models using ANNs are more widely applicable.

2.8 Acknowledgements

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) through an operating grant to R. Pienitz, and by a Marie-Curie-Fellowship awarded to D. Köster. We would like to thank H.J.B. Birks for comments and encouragement in an early stage of this study. We thank Steve Juggins for data discussion and for implementing the new option for WAT in the computer program C^2. Comments and critics by an anonymous reviewer and H.J.B. Birks helped to significantly improve this manuscript.

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3 Paleolimnological assessment of human-induced impacts on Walden Pond (Massachusetts, USA) using diatoms and stable isotopes

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3.1 Résumé

Par l'analyse d'une carotte de sédiment du lac Walden Pond, Massachusetts (États-Unis), son histoire environnementale au cours des derniers 1600 ans a été reconstituée. Les assemblages diatomifères, le pH et le phosphore reconstitués avec des modèles de diatomées, l'abondance des kystes de chrysophycées par rapport à celle des diatomées et la composition géochimique et isotopique des sédiments reflètent l'enrichissement en nutriments du lac suite à la déforestation dans le bassin versant par les colons Européens et, de façon plus prononcée, l'usage récréatif intensif depuis env. 1950 AD. Pendant les dernières 25 années, les assemblages diatomifères se sont stabilisées ce qui suggère que les premières mesures de gestion (limitation du nombre de visiteurs, stabilisation des rives) ont réduit le taux d'eutrophisation. Notre étude montre que les changements observés au cours des dernières 250

années sont exceptionnels dans l'histoire du lac depuis 1600 ans. L'état naturel du lac reconstitué par notre étude représente un bon guide pour les futurs mesures de gestion.

3.2 Abstract

Multi-proxy analysis of a sediment core from Walden Pond, Massachusetts (USA), spanning 1600 years, reveals substantial changes in the nutrient status of the lake over the past ca. 250 years resulting from anthropogenic impacts on the lake and watershed. Following a period of environmental stability from about 430 AD to 1750 AD, the abundance of the diatom *Cyclotella stelligera* increased, the chrysophyte cyst to diatom ratio decreased, organic content declined, bulk organic $\delta^{13}C$ decreased, and bulk organic $\delta^{15}N$ increased. These changes coincided with logging in the lake watershed in the colonial and early industrial periods, and are mainly attributed to an increase in detrital input of inorganic sediment and delivery of dissolved soil decomposition products from the watershed. With the beginning of intensive recreational development of Walden Pond in the mid- 20th century, oligotrophic diatom species were largely replaced by disturbance indicators and the diatom-inferred lake pH increased by 0.5 units, while the bulk organic carbon and nitrogen stable isotope composition markedly shifted to lower and higher values, respectively. These changes reflect inorganic inputs from erosion related to trails, beaches, and building construction, as well as increased nutrient inputs from wastewater seepage into groundwater and extensive recreational use. Diatom-inferred total phosphorus increased only slightly, probably because oligotrophic species persist during spring and autumn, when Walden Pond has lower nutrient concentrations due to reduced recreational activity. During the last 25 years, diatom assemblages stabilized, suggesting that management measures (control of vistor numbers, shore stabilization) have been effective in reducing the rate of eutrophication. Clearly, the changes observed over the past 250 years are well beyond the range of natural variability during the past 1600 years, yet the pre-disturbance record provides a useful benchmark for developing additional restoration and conservation measures to ensure the future health of this historical site.

3.3 Introduction

The evaluation of human disturbance of ecosystems and the development of effective and appropriate restoration and conservation management strategies require knowledge of natural pre-disturbance ecosystem structure. In New England, lakes have been subject to watershed disturbance since European settlement in the 17th century, when forests were cleared for pasture, housing, and wood harvesting (Foster, 1995). Logging, agriculture and urban development in the catchment as well as recreational use have affected water quality in many New England lakes (Siver et al., 1996; Dixit et al., 1999; Francis and Foster, 2001).

Walden Pond, Massachusetts, and its catchment have experienced multiple historical anthropogenic impacts. The site has attracted much attention since the publication of the American classic “Walden” by the natural philosopher Henry David Thoreau (Thoreau, 1854; Whitney and Davis, 1986). Despite the public interest in the protection of the lake as a natural and historical site, few studies exist on the limnology of Walden Pond (Deevey, 1942; Winkler, 1993; Colman and Friesz, 2001) and no comprehensive study of the pre- and post-disturbance limnology of Walden Pond has been conducted. The comparison of historical and recent limnological data suggests that Walden Pond has become more eutrophic since the early 20th century, but there is insufficient data to estimate whether the trophic level has reached a steady state or whether eutrophication continues (Colman and Friesz, 2001).

Paleolimnological studies offer a well-established approach for acquiring pre-historical data on lake water quality (Pienitz and Vincent, 2003). The physical, chemical and biological information preserved in lake sediments provide insight into past events that have occurred within the catchment and their effects on the lake environment. Fossil diatoms, which are well preserved in lake sediments, are useful indicators of past environmental change, including lake trophic status (Moser et al., 1996). By relating limnological data such as total phosphorus (TP) and pH to modern diatom assemblages, diatom inference models have been developed and subsequently applied to fossil samples in order to quantitatively reconstruct past lake properties (Hall and Smol, 1999). Changes in sedimentary diatom composition have been shown to reflect nutrient enrichment following logging and subsequent urban development in the catchments of New England lakes (Davis and Norton, 1978). Diatom-based quantitative reconstructions have been used to infer increased phosphorus and nitrogen concentrations (Siver et al., 1999, Dixit et al., 1999) and rising pH and alkalinity (Davis et al., 1994) in New England lakes since European settlement. The remains of chrysophytes, a group of fossilizing planktonic algae, are also well preserved in lake sediments and are useful indicators of water quality (Zeeb and Smol, 2001). They are used in paleolimnological studies to investigate lake acidification and eutrophication (e.g. Siver et al., 1999).

Lake sediment carbon and nitrogen elemental and stable isotope stratigraphy have been used extensively for assessing changes in lake water nutrient balance in response to the impact of human activities on watersheds. Forest clearance, agricultural activity and urban development in watersheds, for example, frequently lead to lake eutrophication, which is recorded by changes in the carbon and nitrogen elemental and stable isotope composition in lake sediment cores (e.g., Hodell and Schelske, 1998; Schelske and Hodell, 1991, 1995; Brenner et al., 1999; Teranes and Bernasconi, 2000). In some cases, these data also reveal the extent of lake recovery if measures have been taken to reduce nutrient loading, thus serving to evaluate the effectiveness of management strategies (e.g. Schelske and Hodell, 1991, 1995; Hodell and Schelske, 1998).

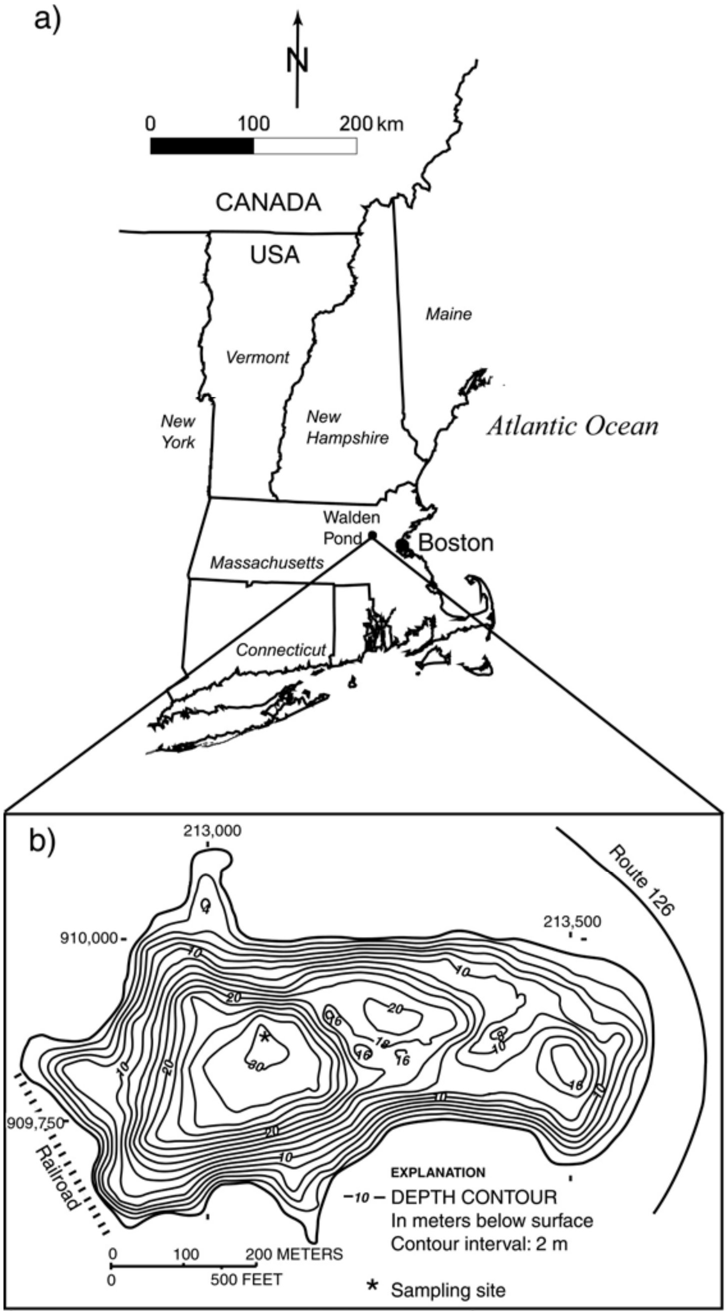
Here we use a multi-proxy paleolimnological approach to assess the impact of human disturbances and of recently adopted management measures on the nutrient balance of Walden Pond over the past few centuries within the context of natural conditions of the past 1600 years. Our efforts focus on 1) the pollen record to document the human impact on the regional vegetation, 2) lake sediment analysis of carbon and nitrogen elemental and isotope geochemistry to qualitatively assess nutrient balance history, 3) the fossil diatom record and diatom-based quantitative inferences for pH and TP to assess the biological response of autotrophic organisms to disturbance, and 4) an evaluation of current management strategies for continued environmental stewardship of Walden Pond based on the results of this study.

3.4 Study site and land-use history

Walden Pond is a 25-ha kettle hole lake in eastern Massachusetts, USA (42°26.3'N, 71°20.4'W; Fig. 3.1a). The present climate is temperate with warm summers (mean July temperature: 21.9°C) and winters allowing the formation of ice cover (mean January temperature: -4.1°C). Presently, 86% of the watershed is covered with Pine-Oak Forest, dominated by *Pinus strobus* and *P. rigida*, as well as *Quercus rubra*, *Q. velutina* and *Q. alba*. The lake consists of three main basins, the eastern shallow basin (max. depth: 18 m), the central basin (max. depth: 20 m) and the deep western basin (max. depth: 30.5 m) (Fig. 3.1b). The watershed (38 ha) is small in relation to the surface of the lake and is characterized by sandy glacial outwash soils and glacial till on granitic bedrock (U.S. Geological Survey). The main water supply (55 %) is groundwater, draining an area of 62.2 ha including a small lake; whereas precipitation contributes 45 % to the water balance (Coleman and Friesz, 2001).

The area was settled by Euopeans at the beginning of the 17th century. The forest around Walden Pond was partly logged for timber, with increasing intensity from the 17th to the 19th centuries (Brian Donahue, Brandeis University, personal communication. Email: bdonahue@brandeis.edu). A slight decline in cutting occurred from 1850 to 1920 with a dramatic decline following the donation of 80 acres surrounding the pond to the Commonwealth of Massachusetts for conservation and open space recreation. A railroad was built in 1844 near the south-western end of the lake. In 1866, an excursion park was built on the shore, which burned down in 1902 and was not rebuilt. In the 1920s, a beach was created at the eastern shore, a bathhouse opened, an amusement park established, attaracted about 500,000 visitors per year. In 1975, the Massachusetts Department of Environmental Management assumed responsibility for managing the park and implemented protection measures including the closure of the amusement park, trail improvement, control of access and improvement of facilities. Presently, the watershed contains a well-developed series of hiking trails and a public beach on the eastern shore, which is frequented by up to 100,000 visitors per month in the summer.

According to recent limnological surveys (Table 3.1), Walden Pond has been characterized as a mostly circum-neutral (mean pH 1997-99: 7.7), oligotrophic to mesotrophic lake with low conductivity (Colman and Friesz, 2001). The highest nutrient concentrations in Walden Pond were measured during the summer (e.g., 140 μg l^{-1}, early September 1989 and 60 μg l^{-1}, late May 1998). Notably, these high values were measured on combined eastern and western basin samples, whereas the highest TP values measured between 1997 and 1999 were 22 μg l^{-1} (May 23, 1998) and 19.5 μg l^{-1} (July 16, 1998) in the western basin, thus indicating that the eastern basin has the highest TP concentrations. Nutrient budgets for the lake indicate that nitrogen (N) inputs are dominated by plume water from the septic leach field of the Walden Pond State Reservation headquarters and the bathhouse (30 %) (both located on the eastern shore of the lake), and possibly by swimmers (34 %). Phosphorus (P) inputs are dominated by atmospheric dry deposition, background groundwater, and estimated swimmer inputs, the latter representing more than 50 % of the P load during summer (Colman and Friesz, 2001). The P budget calculations indicate that the present TP loading is classified between "permissible" and "critical load" according to the Vollenweider model (Colman and Friesz, 2001). The budgets include ground water, atmospheric deposition, swimmers, waterfowl, fish stocking and direct runoff, but exclude internal nutrient recycling. Yet, high N and P concentrations (max. 0.6 mg l^{-1} and 50 μg l^{-1}, respectively) as well as anoxic conditions in the hypolimnion during stratification reveal that nutrients are recycled from the sediments and are introduced to the lake water during full circulation. Comparison with historical DO data collected in 1939 (Deevey, 1942), which recorded an oxygenated hypolimnion, indicates that eutrophication has occurred since then.



Coordinates shown as 500 meter grid, Massachusetts State Plane Projection, 1983

Figure 7 a) Map of the study region. b) Bathymetric map of Walden Pond with coring site. Modified from Coleman and Friesz (2001).

Table 3.1 Limnological characteristics of Walden Pond.
Data for 1994 were obtained at four sampling dates (January, Mai, June, August 1994). Samples were taken from the epilimnion (1 m depth) and the metalimnion (10 m depth) and combined from the eastern and western basins (Baystate Environmental Consultants 1995). Data for 1997-99 are measurements in the western basin: epilimnion and metalimnion (0-14 m depth), taken at 11 sampling dates (May-August 1997; March-September 1998; February 1999) (Colman and Friesz 2001). For calculating minimum (min), maximum (max) and mean values, each sample was used separately, including samples from different depths. The mean N:P ratio for 1997-1999 was calculated from mean total N and mean total P, while minimum and maximum were not calculated because of different sample numbers and depths. The 2001 measurement represents surface water.

Sample date		12/2001	1997-99			1994			1989		
# of samples		1	> 44			16			8		
Sampled basin		west	west			west & east			west & east (combined)		
	Unit		min	max	mean	min	max	mean	min	max	mean
Conductivity	µS cm^{-1}	93	83	92	n.d.	65	87	75	79	87	84
pH		6.9	6.4	9.4	7.7	6.5	7.3	6.8	6	7.7	7
Turbidity	NTU	n.d.	n.d.	n.d.	n.d.	0.43	1.7	1.1	n.d.	n.d.	n.d.
Alkalinity	µg l^{-1}	n.d.	n.d.	n.d.	n.d.	134	182	153	11	12	11
Total phosphorus	µg l^{-1}	5.3	1	22	8.4	10	60	19	10	140	60
Month				May			April			September	
Ammonia	mg l^{-1}	0.02	n.d.	n.d.	n.d.	<0.01	0.14	<0.03	0.02	0.02	0.02
Nitrate	mg l^{-1}	0.03	0.01	0.12	0.04	<0.01	0.05	<0.03	0.02	0.02	0.02
Total Nitrogen	mg l^{-1}	0.33	0.1*	0.57*	0.23*	0.21**	1.1**	0.41**	n.d.	n.d.	n.d.
Secchi depth	m	8.5	2.5	7.5	5.2	4	9.3	6.8	n.d.	n.d.	n.d.
N:P ratio		68:1	n.d.	n.d.	28:1	8.7:1	112:1	22:1	n.d.	n.d.	n.d.
Chlorophyll *a*	µg l^{-1}	2.2	0.1	8.2	2	2.3	3.73	3.1	n.d.	n.d.	n.d.

* = including ammonia. ** = excluding ammonia.

3.5 Methods

3.5.1 Sampling and dating

On February 24, 2000, a 143 cm-long sediment core was extracted from the deep western basin of Walden Pond at a depth of 30 m (Fig. 3.1b), using a simple-tube surface corer. The core was divided into 1 cm thick slices and sub-samples were used subsequently for the analyses of different proxy indicators and dating. The ^{210}Pb chronology (Binford, 1990) was established for the upper 14 cm of the core and by ^{14}C-AMS dating of gyttja at four horizons downcore. The European settlement horizon (ESH) was determined by pollen analysis and has been assigned to the historical recorded date 1635 AD for the foundation of the town of Concord (Wheeler, 1967). The complete chronology was calculated by interpolation between the depths of known ages using exponential trend lines.

3.5.2 Pollen

Sediment preparation for pollen analysis followed standard procedures (Faegri and Iversen, 1975). Pollen was counted to a total of 500 tree and shrub grains at 400x magnification. Pollen percentages are based on total terrestrial pollen grains, excluding aquatics, but including agricultural grains (i.e. herbs). Identification is based on standard taxonomic keys (McAndrews et al., 1973; Moore et al., 1991).

3.5.3 Organic matter, carbon and nitrogen elemental and stable isotope geochemistry

Organic matter was measured at 1 cm intervals using standard loss-on-ignition procedures (Dean, 1974). Approximately 1 cm^3 of wet sediment was dried overnight at 95 °C and then weighed before and after combustion at 550 °C for one hour.

Sediment sub-samples were analysed at 4 cm intervals for bulk organic carbon and nitrogen elemental and stable isotope geochemistry composition. Samples were acid-washed in 10% HCl to remove carbonates, rinsed with de-ionized water and freeze-dried. Coarse-grained

(>500 mm) sediments were removed by sieving. The fine-grained fraction was analysed for organic carbon and nitrogen percent and stable isotope composition using a Micromass Isochrom continuous flow mass spectrometer equipped with an elemental analyser at the University of Waterloo - Environmental Isotope Laboratory. Carbon and nitrogen isotope composition are reported in δ-notation, such that $\delta = [Rsample/Rstd - 1] \times 1000$ where R is the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in the sample and VPDB and AIR standards, respectively. Analytical uncertainty is ± 0.03 ‰ for $\delta^{13}C$ and $\delta^{15}N$ based on repeated analyses of several samples.

3.5.4 Diatom and chrysophyte analyses

Samples for diatom analysis were processed using standard procedures (Pienitz et al., 1995). A minimum of 500 valves per sample were counted and identified according to Camburn and Charles (2000), Krammer (1986-1991), and Fallu et al. (2000). The taxonomy of the fossil and modern samples were matched by personal communication with S. Dixit and by comparing our photographs with figures presented in Camburn et al. (1984-86), as this was the main taxonomic reference used by Dixit et al. (1999) for the training set. Chrysophyte cysts were counted, but not identified, and the scales of synurophytes (a group of chrysophytes) were counted and partly identified on the same slides as the diatoms. The ratio of chrysophyte cysts and scales to diatom frustules are expressed as the percentage of the respective remains related to the sum of diatom frustules (= half of the diatom valve count) and the total count of chrysophyte remains.

Fossil diatom assemblages were subdivided into stratigraphic zones by optimal partitioning using the computer program ZONE (S. Juggins, unpublished program). The significant number of zones was estimated by the broken stick model (Bennett, 1996). However, this zonation technique separates groups at the midpoint of gradual changes, which does not always reflect the timing of the onset of change. Therefore, we assigned the border between Zone II and Zone III to the level where the change began (12 cm instead of the calculated 10 cm), in order to relate the start of this change to historically recorded human disturbances.

3.5.5 Numerical analysis for diatom-based environmental reconstructions

For quantitative reconstructions of pH and TP, we used transfer functions based on limnological and subfossil diatom data (Dixit et al., 1999) from 82 lakes located in the states of Vermont, New Hampshire, Massachusetts, and Connecticut (Köster et al., in press). Details concerning numerical analyses of the data set, model development, and comparison of quantitative reconstructions with the instrumental record of Walden Pond are presented in Köster et al. (in press). Diatom-based inference models based on weighted averaging with inverse deshrinking (WAinv) (Table 3.2) were used for the reconstructions in this study, as they represented the simplest models with good statistical performance (Köster et al., in press). Model development, environmental reconstructions and calculation of sample-specific errors for the fossil samples were carried out using the program C^2 (Juggins, 2003). Errors were estimated by bootstrapping, an intensive cross-validation procedure.

Table 3.2 Performance of the pH and total phosphorus models used for paleolimnological reconstructions in Walden Pond. Models are based on diatom and environmental data from 82 New England lakes (Dixit et al. 1999).

Gradient	method	r^2	RMSE	r^2_{boot}	RMSEP	max. bias
pH	WA inv.	0.87	0.24	0.81	0.33	0.57
TP	WA inv.	0.47	0.20	0.35	0.28	-0.54

In order to test how well the fossil diatom assemblages are represented in the model data set, two methods of analog measures are applied. The coefficients of dissimilarity using chord distance (Overpeck et al., 1985) were calculated using the program ANALOG (H.J.B. Birks and J.M. Line, unpublished program). Based on the mean minimum dissimilarity coefficient (DC) within the model data, the 75% and 95% confidence intervals were calculated (Laird et al., 1998). Fossil samples with a DC lower than the 75% confidence interval were deemed to have good analogs in the calibration set, whereas DCs between 75% and 95% indicated poor analogs and DCs outside the 95% interval indicated no analogs (Laing et al., 1999). Furthermore, the “goodness of fit” of the fossil assemblages to the reconstructed variables pH and TP was evaluated by a CCA with the first axis constrained to one variable and defining the modern and fossil samples as active and passive, respectively. Fossil samples having residual distances to the first axis outside the 95% confidence interval of the modern samples' distances were considered to have very poor fit (Birks, 1990).

3.6 Results

3.6.1 Chronology and lithology

The chronology of the sediment core, based on ^{210}Pb (appendix: Fig. A.1) and ^{14}C dates as well as the European settlement horizon (Table 3.3, Fig. 3.2), indicates a sedimentation rate of about 0.13 cm/ year from ca. 430 to 1200 AD. From ca. 1200 to 1700 AD, sediment accumulation declined to 0.04 cm/year, rising to an average rate of 0.09 cm/year over the last 300 years.

The organic content of the sediments, inferred from loss-on-ignition, remains relatively constant with values around 40% from ca. 430 to 1500 AD, except at ca. 670 AD (100 cm) where a value of 49% was obtained (Fig. 3.4 a). At ca. 1600 AD, the percentage of organic matter begins to decline, until it reaches about 25% at ca. 1960 AD. Afterwards, the proportion of organic matter fluctuates between 25% and 40% with a tendency to higher levels in the most recent sediments.

Table 3.3 ^{14}C dates for Walden Pond including AMS dates in years BP (ybp), calibrated dates (cal ybp) and calibrated dates converted to calendar years.

depth (cm)	ybp	calibrated ybp	lab error	2 sigma error	cal ybp + 50	^{14}C converted to calendar years (2000 - cal ybp + 50)
44-45	785	689	35	80	739	1261± 80
60-61	1084	970	35	110	1020	980 ± 110
90-91	1301	1261	36	120	1311	689 ± 120
124-125	1517	1396	38	96	1446	554 ± 96

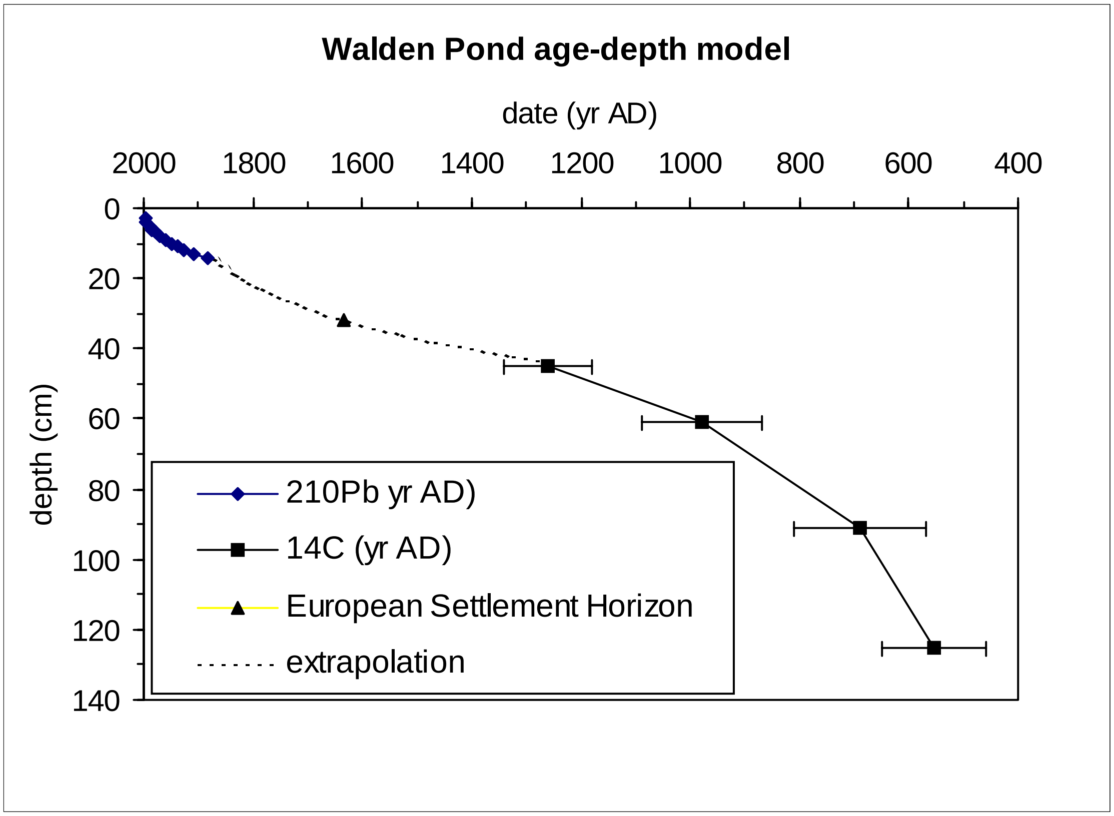


Figure 8 Age-depth model for Walden Pond.
Dates were established by the ^{210}Pb and ^{14}C method. The European settlement horizon (ESH) was determined by pollen analysis and has been assigned to the historical recorded date 1635 AD. The dates for the samples between the dated horizons were calculated by extrapolation using an exponential trend line.

3.6.2 Pollen

Before European settlement, *Quercus* (oak), *Pinus* (pine) and *Betula* (birch) dominated the pollen stratigraphy, with about 15% aquatic macrophytes, and no significant changes in relative pollen abundances were observed (Fig. 3.3). After European settlement in the early 17th century, the proportion of *Pinus* increased from 15 % to 25 % and the amount of agricultural weeds (including *Poaceae, Ambrosia, Rumex*, etc.) increased. Between ca. 1840 and 1900 AD, the abundance of *Quercus* decreased by 20 - 30 %, *Pinus* declined and agricultural weeds increased until peak proportions of 28 %. In the early 20th century, *Betula* showed a maximum of 28 % and herbs declined sharply. Shortly afterwards *Betula* declined coincident with increases of *Quercus* and *Pinus*. *Fagus* (beech) and *Tsuga* (hemlock) pollen declined gradually from the early 18th century until present. Between 10 and 8 cm (ca. 1940–1960 AD), the relative abundance of aquatic macrophytes, mainly *Isoetes* (Quillworth), declined rapidly from 11 to 1.5%.

3.6.3 Carbon and nitrogen elemental and stable isotope stratigraphy

The carbon and nitrogen elemental and isotope stratigraphy of Walden Pond was generally stable until marked changes occurred at the top of the core above about 24 cm depth (after ~ 1770 AD), corresponding with the main period of human disturbance in the catchment (Fig. 3.4). Organic carbon and nitrogen content in sediments below these strata were near constant with values of 20 and 2 %, respectively (Figs. 3.4 b, c). Above this horizon, C and N rapidly declined to values as low as 16.8 and 1.2 %, respectively, and then increased to values similar to those observed in the pre- ~ 1770 AD interval. A brief increase in C % at 12.5 cm depth (~ 1910 AD) interrupted this general trend and corresponds to a horizon rich in charcoal fragments. Similarly, $\delta^{13}C$ and $\delta^{15}N$ were also generally stable in the lower strata with values of about -26.5 and 1.5 ‰, respectively (Figs. 3.4 d, e). Around 1770 AD, $\delta^{13}C$ values began to decline substantially to -30 ‰, whereas $\delta^{15}N$ values markedly began to increase to 5 ‰. Unlike the trends observed in the elemental profiles, the carbon and nitrogen isotope values did not return to values observed in the pre- ~ 1770 AD interval.

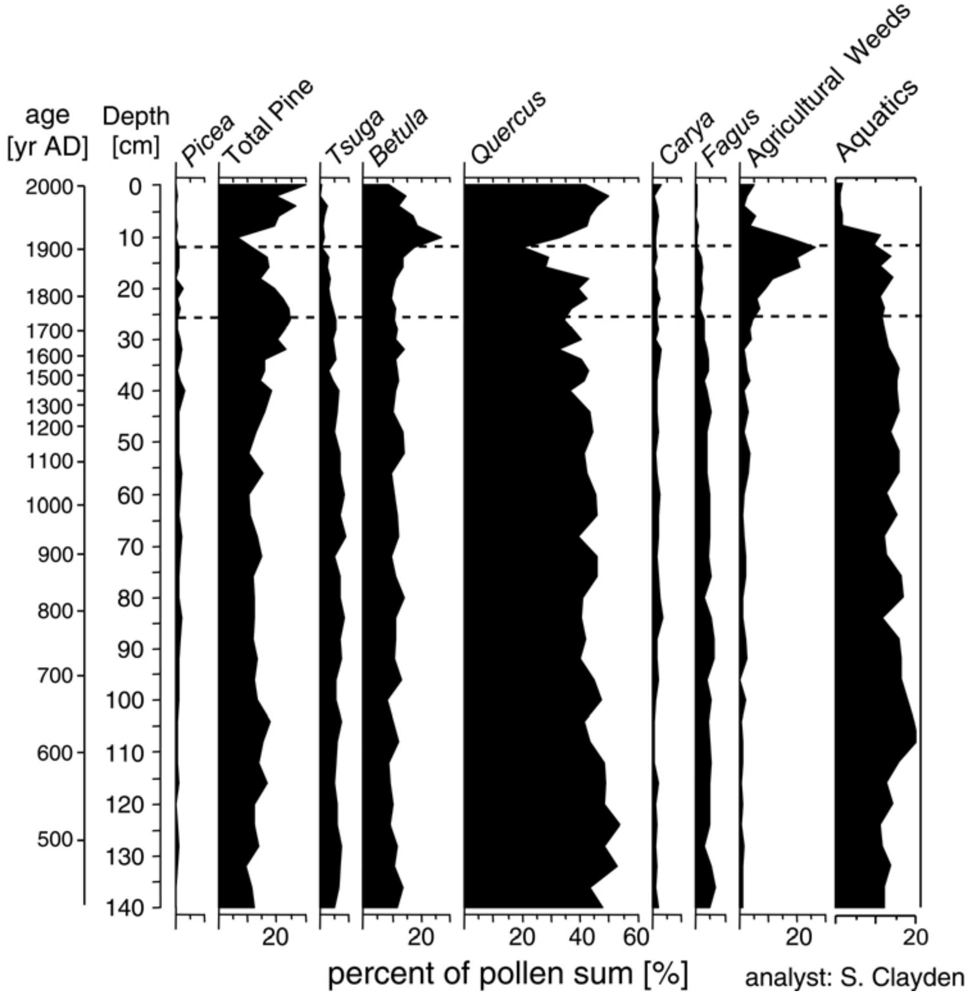


Figure 9 Pollen stratigraphy of selected taxa for Walden Pond.
Abundances of aquatic taxa were calculated as percentage of total non-aquatic pollen and were not included in the calculation of pollen percentages. Dashed horizontal lines indicate the major diatom zones (see Fig. 3.5).

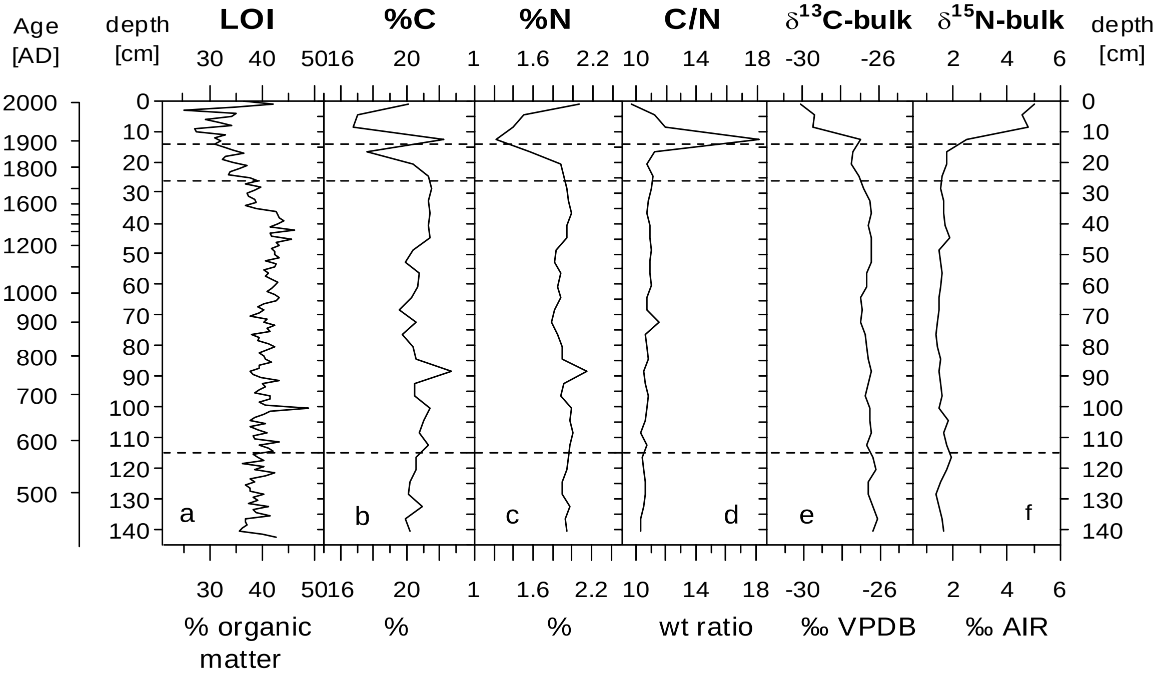


Figure 10 Loss-on-ignition (a), bulk organic carbon and nitrogen elemental (b, c, d) and stable isotope stratigraphy (e, f) for Walden Pond.
Dashed horizontal lines indicate the major diatom zones (see Fig. 3.5).

3.6.4 Diatom and chrysophyte stratigraphy

Three major periods with differing diatom assemblages were distinguished for the last ca. 1600 years, including one zone preceding European settlement and two zones after ca. 1750 AD, the latter two corresponding to human disturbance in the watershed (Fig. 3.5).

3.6.4.1 Zone I (140-26 cm, ca. 430 to 1750 AD)

In Zone I, the oligotrophic to mesotrophic and circumneutral to acidophilic species *Tabellaria flocculosa* (Roth) Kütz. str. IIIp sensu Koppen and *Cyclotella stelligera* (Cleve and Grunow) Van Heurck dominated. The acidobiontic diatom *Asterionella ralfsii* var. *americana* Körner was present at low abundance throu*ghout this period. Fragilaria nanana Lange-Bertalot and Cyclotella bodanica aff.* lemanica (Müller ex Schröter) Bachmann were present with abundances less than 10%. The ratio of chrysophyte scales to diatom frustules varied between 9 and 29% (mean: 18%, Fig. 3.5). The ratio of chrysophyte cysts to diatoms ranged from 7 to 21% (mean: 13%), with the highest values (18 to 20%) around 1700 AD.

3.6.4.2 Zone II (26-12 cm, ca. 1750 to 1920 AD)

Around 1750 AD, the abundance of *T. flocculosa* str. III p started to decline, while *C. stelligera* increased by about 30%. *Cyclotella bodanica* aff. *lemanica* decreased from around 10% to very low abundance at ca. 1860 AD. The synurophyte scales to diatom frustules ratio remained constant (mean 21%), however, the mean relative abundance of chrysophyte cysts decreased from 13% to 8%.

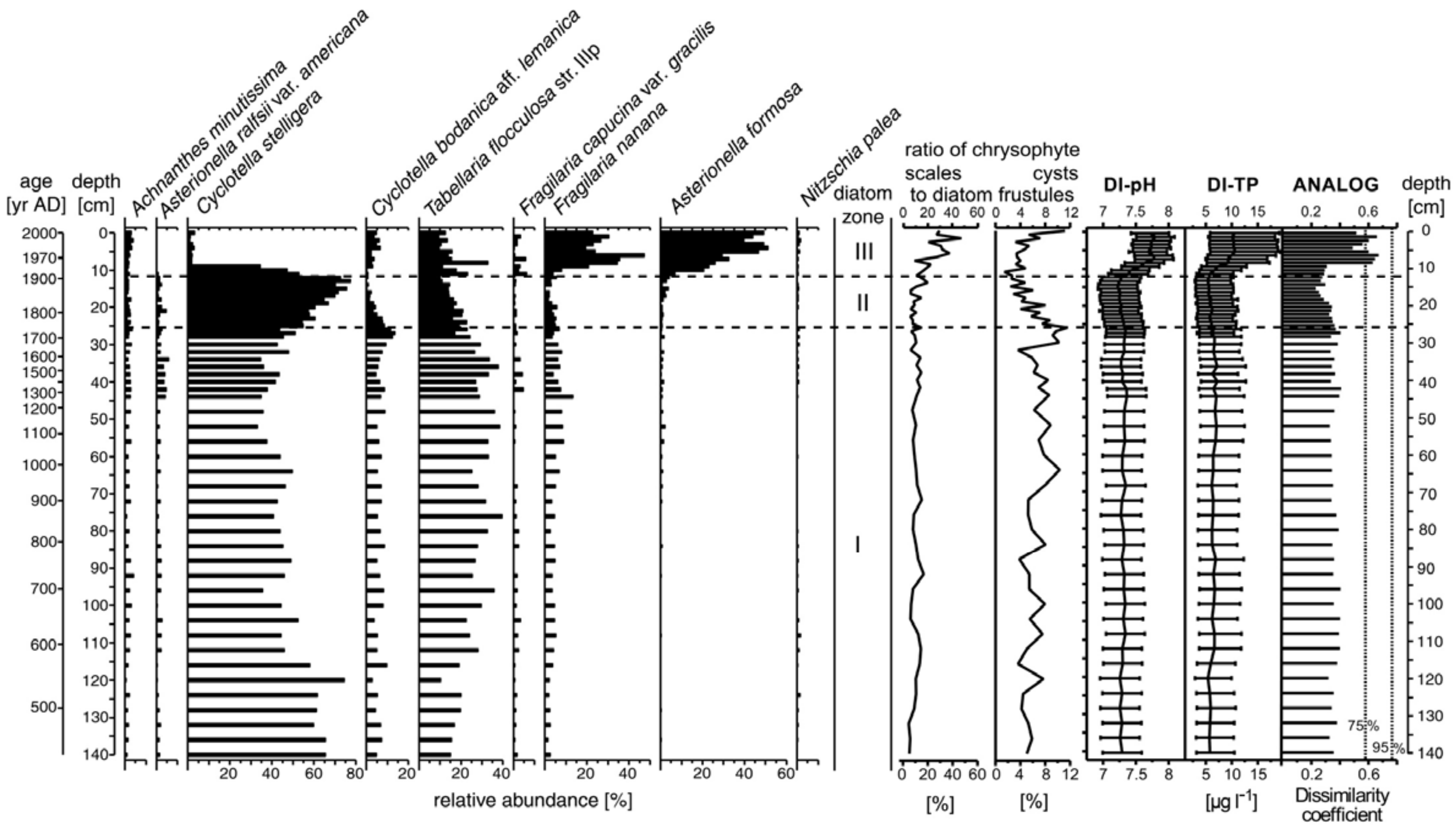


Figure 11 Diatom stratigraphy of Walden Pond with major zonation, ratio of chrysophyte scales and cysts to diatom frustules, diatom-inferred pH (DI-pH) and TP (DI-TP) and analysis of dissimilarity using the program ANALOG.
The sample-specific errors for DI-pH and DI-TP (for TP back-transformed to $\mu g \cdot l^{-1}$) are indicated by horizontal bars. Dashed vertical lines in the ANALOG graph indicate the 75% and 95% confidence limits. Values lower than the 75% limit indicate good analogs, values between the 75% and the 95% limit indicate poor analogs.

3.6.4.3 Zone III (12-0 cm, ~ 1920 to 2000 AD)

In the early 20th century, diatom assemblage composition showed a striking change. The abundances of the disturbance indicators *Asterionella formosa* Hassal and *Fragilaria nanana* increased from about 5% in the late 19th century to 50 and 35% respectively in the ~ 1960s. Simultaneously, *Cyclotella stelligera* decreased rapidly, from a maximum abundance of 77% at ~ 1900 AD to an average abundance of 3% after ~ 1930 AD whereas *C. bodanica* aff. *lemanica* and *T. flocculosa* str. IIIp remained relatively constant at ca. 5% and 15%, respectively. *A. ralfsii* var. *americana* disappeared around 1940 AD and was not subsequently recorded. From about 1980 to 2000 AD this new diatom assemblage stabilized.

The mean chrysophyte scales to diatom frustules ratio increased to 43%, with a maximum of 64% in ~ 1998. This increase was mainly caused by much higher abundances of scales of *Mallomonas crassisquama*. The ratio of chrysophyte cysts to diatom frustules remained low with values around 8% until about 1997, and then increased to 10-20% in the upper three levels.

3.6.5 Quantitative reconstructions of pH and TP

Two major periods with differing analog situations prevail in the sediment core (Fig. 3.5). The samples between 140 cm and 9 cm (ca. 430 to 1950 AD) have dissimilarity coefficients lower than the 75% confidence limit, indicating that the fossil diatom species are well represented in the model data set. With the exception of the samples at 4, 3 and 0 cm, the recent samples between 8 and 0 cm (ca. 1950 to 2000 AD) have dissimilarity coefficients between the 75% and 95% critical values, indicating poor analogs. Similar patterns were obtained by the "goodness of fit" analysis using CCA. The samples from 140 to 9 cm have a good fit to pH and TP, whereas the levels 8 to 0 cm lay outside the 95% confidence limit, indicating a poor fit of those samples to both variables (Fig. 3.5).

The diatom-inferred values of pH (DI-pH, Fig. 3.5) remained stable from ca. 430 to 1880 AD, with values fluctuating around 7.3. Afterwards, the DI-pH sharply increased to 7.8 at ca. 1970 AD, after which values stabilized until the present day.

The diatom-inferred TP (DI-TP, Figure 5) followed similar trends as DI-pH, but increased with a time lag of about 50 years. DI-TP remained relatively stable with values around 6 mg l^{-1} in the lower levels until ca. 1930 AD. Thereafter, DI-TP continuously increased in recent sediments, reaching a maximum of 10 mg l^{-1} in the 1970s, and remained stable afterwards. The magnitude of these inferred changes, however, remained inside the error range of lower core samples.

3.7 Discussion

3.7.1 Pollen

Major patterns in sedimentary pollen assemblages (Fig. 3.3) reflect regional land-use history. High abundances of agricultural weeds and parallel declines of tree species from ca. 1800 to 1900 AD are likely associated with the regional deforestation for agriculture and town growth. Pollen abundances of *Fagus* and *Tsuga* also decreased after 1700 AD due to land clearance, timbering and fire. A peak of the pioneer tree birch in the early 20th century and a subsequent increase of dominant pre-disturbance species of the genera *Quercus* and *Pinus* reflect the regional re-growth of forest.

The clear decline of aquatic macrophytes (*Isoëtes*) spores between 1940 and 1960 AD may be related to changes in water transparency. Today, water transparency is relatively high (Secchi depth: 2.5 - 9 m), thereby permitting growth of aquatic macrophytes, mainly the macroalga *Nitella*, between 6 and 13 m water depth (Colman and Friesz, 2001). Deevey (1942) observed a very high water transparency in 1939, with aquatic mosses found at 15.7 m water depth. Therefore, a moderate decline in transparency may have taken place since then.

3.7.2 Carbon and nitrogen cycling

Fundamental to the interpretation of organic geochemical records in lake sediments is knowledge of the origin of the organic matter. In the Walden Pond sediments, the fine-grained organic matter fraction is predominantly of aquatic origin based on the C/N ratios of near 10 throughout the record (cf., Meyers and Lallier-Verges, 1999). The only exception is the charcoal-rich horizon at 12 cm (~ 1910 AD), which correspondingly has an elevated C/N ratio of 18.2 and is consistent with organic matter derived from terrestrial sources (Fig. 3.4 d).

Human disturbance since about 1770 AD has evidently had a dramatic impact on the nutrient balance of Walden Pond. Large changes observed in the carbon and nitrogen elemental and stable isotope stratigraphy are clearly beyond the range of natural environmental variability observed over the last ~ 1600 years. Initial removal of catchment vegetation by logging appears to have resulted in an influx of primarily inorganic sediment, based on the decline in % C and % N (Fig. 3.4 b, c). Although the decline in organic content could also be interpreted as a reduction in lake productivity, this is less likely given the increase in catchment-derived nutrient loading that probably occurred during European settlement and which has been suggested elsewhere in the region (e.g., Kaushal and Binford, 1999; Hilfinger et al., 2001).

The subsequent increase in organic content at the top of the core may reflect a very recent increase in lake productivity. Alternatively, erosion protective measures in the catchment may be responsible for a reduction in the amount of inorganic sediment entering the lake or this sample may represent freshly deposited sediment that has not undergone degradation.

A number of factors can influence the carbon and nitrogen stable isotope composition of organic matter. For carbon, these primarily are processes that determine the carbon isotope composition of lake water dissolved inorganic carbon (DIC), the source of carbon for aquatic plants. These processes include the lake productivity-respiration balance, CO_2 exchange between the lake water DIC and the atmosphere, and the carbon isotope composition of DIC derived from the catchment produced during soil respiration and bedrock weathering (Boutton, 1991). The carbon isotope fractionation between the carbon source and aquatic plants can also vary depending mainly on the dissolved CO_2 concentration and HCO_3^- uptake (Hodell and Schelske, 1998). Similarly, the nitrogen isotope composition of organic matter is dependent on several factors, including productivity, nitrogen transformations in the water column (e.g., denitrification, ammonium volatilization), and the nitrogen isotope composition of dissolved nutrients (Talbot, 2001).

Changes in carbon and nitrogen stable isotope records of lakes that have undergone catchment disturbance are frequently attributed to shifts in carbon and nitrogen cycling resulting from increased nutrient loading (Teranes and Bernasconi, 2000; Wolfe et al., 2000; Herczeg et al., 2001). Indeed, trends toward lower δ^{13}C and higher δ^{15}N values in the initial post-1770 AD interval (Figs. 3.4 e, f) are also most likely associated with increased nutrient supply from the removal of vegetation in the catchment and, in particular, increased delivery of ^{13}C-depleted dissolved CO_2 and ^{15}N-enriched NO_3^- from soil decomposition processes. Alternatively or in addition, productivity-driven enrichment of the dissolved inorganic nitrogen (DIN) may have contributed to the positive shift in δ^{15}N in the lake sediment record. Evidently, similar productivity-driven enrichment of the DIC did not occur in Walden Pond perhaps due to a larger lake water reservoir of DIC compared to DIN. During the past 70 years, these trends have accelerated well beyond the range of natural variability observed over the past 1600 years and are possibly related to ^{13}C-depleted and ^{15}N-enriched wastewater seepage into the lake, although additional sampling of carbon and nitrogen isotope composition of the wastewater at Walden Pond is required to test this hypothesis.

3.7.3 Diatom paleolimnology

The changes in fossil diatom and chrysophyte assemblages observed in Walden Pond sediments (Fig. 3.5) are likely related to the human-induced changes in nutrient balance at Walden Pond over the past two centuries, as evidenced by comparison of biostratigraphic changes with those revealed by the carbon and nitrogen elemental and stable isotope record.

3.7.3.1 Zone I (140-26 cm, ca. 430 to 1750 AD)

The dominance of the diatom taxa *Cyclotella stelligera* and *Tabellaria flocculosa* str. III p and the presence of *Asterionella ralfsii* and *Cyclotella bodanica* aff. *lemanica* indicate that Walden Pond was an oligotrophic, circumneutral to slightly acidic lake between ca. 430 and 1750 AD. The low nutrient content can be explained by the naturally nutrient-poor soils in the catchment and the relatively small watershed from which not much terrestrial material is washed into the lake, as reflected by low C/N ratios. The fossil diatom flora consists mainly of planktonic species, which may be expected in a core taken from the deepest part of the lake, where higher planktonic: benthic diatom ratios are likely to occur.

3.7.3.2 Zone II (26-12 cm, ca. 1750 to 1920 AD)

The decrease of *T. flocculosa* str. III p and the increase of *C. stelligera* between ca. 1750 and 1900 AD coincide with the first known anthropogenic disturbance by timber harvesting in the Walden Pond watershed. The proportion of herbal pollen increased significantly at the same time, from 5% to 30% (Fig. 3.3), indicating an opening of the forest vegetation in the region. Additionally, the decreases in sediment organic matter, % C, and % N (Fig. 3.4a-c) suggest higher mineral inputs through soil erosion caused by logging activities.

Cyclotella stelligera similarly increased following forest clearance in the watershed of British Columbia lakes (Laird and Cumming, 2001), in Michigan lakes (Fritz et al., 1993) and in a Swiss lake (Lotter, 2001) as well as in Adirondack lakes (Rhodes, 1991). Logging in the watershed can lead to nutrient enrichment of lakes (Lott et al., 1994; Carignan et al., 2000). Engstrom et al. (1985) and Stoermer et al. (1985) related higher *Cyclotella* abundances, including *C. stelligera*, to nutrient enrichment. Other studies have indicated that *C. stelligera* may reflect re-oligotrophication (Clerk et al., 2000) and Brugam (1989) reported its decline after almost complete deforestation of Washington lake watersheds. These results suggest that the increasing abundance of *C. stelligera* after ca. 1750 AD reflects the removal of vegetation in the catchment of Walden Pond by logging activities, but that its abundance may decline with further nutrient enrichment.

There is no obvious explanation for the decrease of *Tabellaria flocculosa* str. III p, as other studies have shown that this taxon can increase (Stoermer et al., 1991) or decrease (Dixit et al., 1996) following lake nutrient enrichment, probably showing a similar response as *C. stelligera*. In fact, the decrease of relative abundances of *T. flocculosa* str. III p at Walden Pond occurred simultaneously with the increase of *C. stelligera*, thus it may only have declined in relative numbers.

The decrease in the chrysophyte cyst : diatom frustule ratio between ca. 1750 and 1920 supports the hypothesis of a slight nutrient enrichment. Decreasing abundances of chrysophyte cysts relative to diatoms in lake sediments have been proposed to accompany lake eutrophication (Smol, 1985).

3.7.3.3 Zone III (12-0 cm, ca. 1920 to 2000 AD)

The striking change from a diatom assemblage associated with oligotrophic conditions and with moderate catchment disturbance, such as discussed above, to one dominated by disturbance indicators, such as *Asterionella formosa* and *Fragilaria nanana,* is likely related to additional nutrient supply derived from increased activity in the watershed (i.e., trail and beach development, railway construction, wastewater seepage, and other recreation activities) over much of the past century. Nutrient-enriched lakes are often characterized by increased abundances of *A. formosa* (e.g., Pennington, 1981; Bennion et al., 2000) and larger *Fragilariaceae*, such as *Synedra delicatissima* W. Smith (Brugam, 1978), *Fragilaria crotonensis* Kitton (Reavie, 2000; Lotter, 2001), *F. nanana* (Reavie et al., 1995), and *S. nana* Meister (Bennion et al., 2000).

The diatom species shift found in recent sediments probably relates to changes in summer conditions. According to a phytoplankton record of Walden Pond in 1995, *A. formosa* and *Synedra* spp. (likely synonymous with *Fragilaria* spp.) grow during summer in this lake (Baystate Environmental Consultants, 1995). However, *Asterionella* and *Fragilaria* are also common during spring and autumn in lakes throughout North America. The explanation for this difference may be found in the unusual combination of preservation and recreational use of Walden Pond. During most of the year, the lake is almost undisturbed because of the forested watershed and the absence of private houses, whereas during the few summer months there are thousands of visitors to the lake, who contribute approximately 27% of the annual P load and 64% of the annual N load (Colman and Friez, 2001). Continuing nutrient (e.g., phosphorus) availability and sufficient epilimnetic mixing throughout the summer may permit diatoms to form a richer summer population (Sommer et al., 1986). Maximum nutrient concentrations at Walden Pond were measured in summer in the eastern basin, close to the beach (Table 3.1). Therefore, it is possible that reacreational activities in the summer are the source for nutrients that support a summer diatom population. This was likely different under the oligotrophic conditions that prevailed during periods preceding anthropogenic disturbances because phosphorus would have been largely consumed by spring blooms.

Cyclotella stelligera is also a summer species, yet it is out-competed by *A. formosa* and *Fragilaria* spp. which are good competitors for phosphorus (VanDonk and Kilham, 1990) and which have been shown to be favoured by high total N:total P ratios (Interlandi et al., 1999). The high N:P ratio of 40:1 (average January to August values in the epilimnion and metalimnion, Baystate Environmental Consultants, 1995), indicates that phytoplankton growth is phosphorus-limited in Walden Pond. The proposed association between diatom disturbance indicators with summer conditions in Walden Pond (see above) requires testing from comprehensive phytoplankton surveys of the lake over several years and including all seasons. Also, as most nutrient inputs enter the lake on the eastern shore, a more detailed analysis of the eastern basin is necessary to completely characterize the lake's limnology.

The higher relative abundance of synurophyte scales in the recent sediments (Fig 3.5), mainly produced by *Mallomonas crassisquama,* supports the hypothesis of a nutrient enrichment of Walden Pond. This species also proliferated following nutrient addition to an Experimental Lake in western Ontario (Canada) (Zeeb, 1994). Preliminary counts of synurophyte scales in another core, taken at Walden Pond in 1979, showed striking changes in species composition at about 1900 AD (John P. Smol, personal communication), coincident with the major change in the diatom assemblages in zone III. Taxa associated with undisturbed conditions and that are now quite rare, such as *Mallomonas lelymene* and *M. allorgei*, dominated the pre-disturbance sediments. In the recent sediments, they were replaced by taxa indicating higher nutrient availability, such as *M. elongata* and *M. caudata.* Thus, the changes in chrysophyte populations also reflect the nutrient enrichment of Walden Pond.

The chrysophyte cyst proportions remained lower during the 20th century than during pre-settlement times, indicating a higher trophic state. The upper three samples (1995-2000 AD) showed increasing proportions, indicating decreasing nutrient concentrations. The stability in chrysophyte cyst proportions during the early 20th century seems to contradict the increasing synurophyte scale : diatom ratio at the same time. The explanation may be that only the Synurophyceae form scales, such as the dominant *Mallomonas crassisquama* in the recent sediments of Walden Pond. However, cysts are formed by scaled and non-scaled taxa from several chrysophyte groups. It is therefore possible that scales were more abundant due to this scaled species following nutrient enrichment, but that overall chrysophyte and cyst abundances (consisting mainly of oligotrophic species) remained low.

During the last ca. 20 years, diatom assemblages seem to have stabilized, probably indicating a reduced rate of eutrophication. As first management measures for water quality protection were implemented in 1975, these measures may have indeed reduced the nutrient loading to Walden Pond during summer.

3.7.4 Quantitative reconstructions of pH and TP

Analog and Goodness-of-fit analyses have shown that the reconstructions are reliable for all levels, with the exception of levels 0-8 cm. Poor analogs and fit were detected for these uppermost levels, although all dominant fossil species are present in the model. The poor analogs result from high abundances of few species in our fossil samples (e.g. *Fragilaria nanana*, *Asterionella formosa)*, which is not the case in the training set lakes, where these species are present at lower abundances. This is likely due to higher relative abundances of benthic taxa in the training set lakes, which are generally shallower than Walden Pond. We assume that useful ecological parameters (species optimum and tolerance) have been estimated for the models and that they are therefore appropriate for inferring pH and TP in our sediment core.

From ca. 430 to 1880 AD (diatom zones I and II), diatom-inferred pH and TP remained constant, reflecting the stable diatom assemblages (Fig. 3.5). The DI-TP of 5-6 $\mu g\ l^{-1}$ indicated oligotrophic conditions. The circumneutral character of the dominant species was reflected by the DI-pH, which fluctuates between 7.2 and 7.3.

A rapid increase in DI-pH by 0.5 units occurred between ca. 1920 and 1960 AD, reflecting the abrupt change in species composition from zones II to III. A rise in pH may indicate higher primary productivity in the lake. Phytoplankton and macrophytes remove CO_2 from the water column by photosynthetic assimilation, thereby driving the bicarbonate balance towards the alkaline end. pH measurements in recent years have shown peak values of 9 and more in the epilimnion during summer (Colman and Friesz, 2001), suggesting a temporally alkaline environment generated by high primary productivity.

Alternatively, pH can increase due to higher base cation concentrations (i.e. higher alkalinity). The source of such ions can be diverse: soluble inorganic material (Mg^{2+}, Ca^{2+}) may be washed into the lake by runoff over eroded soils, as suggested by lower organic nitrogen and carbon contents in the sediments beginning in zone II and persisting through zone III. An explanation for an increase in alkalinity may also be the higher in-lake productivity attributable to higher nutrient levels from logging and recreational use as discussed above. Increased deposition of organic material causes oxygen depletion in the hypolimnion of Walden Pond during late summer and autumn (Baystate Environmental Consultants, 1995; Colman and Friesz, 2001; Köster, unpublished data) permitting sulphate reduction and denitrification in the hypolimnion, as well as release of base cations from sediments (Schindler, 1986; Psenner, 1988). Manganese, iron, phosphorus and ammonia concentrations were high in the hypolimnion near the sediments in late summer (Colman and Friesz, 2001), indicating that alkalinity was in fact generated in the anoxic hypolimnion and at the sediment/water interface.

Higher DI-TP values in the top of the core support the evidence of rising nutrient levels at Walden Pond, which was provided by stable isotopes and chrysophytes. However, this change is subtle with 5 $\mu g\ l^{-1}$. Given the drastic changes in diatom species composition, and changes in geochemistry and stable isotope composition that were attributed to an increase in nutrient loading, the small increase in diatom-inferred TP is surprising. However, the reconstructions correspond well with the instrumentally recorded mean annual total phosphorus levels in the western basin that remained below 10 $\mu g\ l^{-1}$ between 1997 and 1999 (Table 3.1). Yet, some summer samples during this time show a deviation from the mean (ca. 20 $\mu g\ l^{-1}$; Table 3.1). The shift in the diatom community of the western basin to one dominated by species typical of nutrient-enriched waters is probably due to these moderate seasonal phosphorus maxima, as discussed above. During seasons when Walden Pond is not subject to intense recreational use (e.g., spring and autumn) the lake water returns to lower nutrient concentrations (<10 $\mu g\ l^{-1}$), probably allowing proliferation of diatoms with low TP optima, such as *Cyclotella bodanica* and *Tabellaria flocculosa* str. III p. For quantitative reconstructions based on fossil samples that integrate all seasons, this means that species with low-TP optima may partly balance out the effects of species with high TP optima growing during summer.

3.7.5 Implications for the management of Walden Pond

Although the lake is presently considered to be oligo- to mesotrophic and its clear water suggests a “natural state”, the geochemical and diatom records in the sediments of Walden Pond indicate substantial changes in the nutrient balance of the lake due to human impact during the last three centuries. The low susceptibility of the lake to exhibit evident signs of eutrophication, such as turbid water caused by phytoplankton blooms may be due to its great depth, its small watershed, and the fact that it is mainly fed by groundwater. Human-derived nutrients added to the lake in the summer may be used up by planktonic organisms, which subsequently transfer the nutrients by sedimentation to the lake bottom. However, increased nutrient inputs to Walden Pond through erosion and recreational use during much of the 20th century have left a signature in the lake sediments, which have the potential of being recycled into the lake water column. Active bacteriological decomposition of organic matter leads to oxygen-depleted conditions in the hypolimnion of the lake in late summer and autumn, permitting recycling of sedimentary nutrients to the water column and up-welling during full circulation periods. If high nutrient inputs during summer persist, past and present nutrient loads may lead to further eutrophication of Walden Pond.

Stable diatom assemblages and increasing chrysophyte cyst proportions in the uppermost sediments suggest that initial management practices applied in the 1970s have halted the process of eutrophication. Current preventive measures to reduce nutrient loading including the monitoring of groundwater down gradient from the septic leach field and of oxygen content in the hypolimnion, storm water runoff control, and public awareness activities (Colman and Friesz, 2001) should therefore continue. If signs of further eutrophication, such as more frequent anoxia in the hypolimnion, are observed, or if nutrient contamination of the groundwater starts to increase, more effective wastewater treatment and reduced recreational usage may be necessary to protect Walden Pond from further water quality deterioration.

3.8 Conclusions

Multiple anthropogenic disturbances in the watershed of Walden Pond over the past ca. 250 years have had a marked impact on the nutrient balance of Walden Pond as evidenced by the paleolimnological record. First changes in diatom assemblages and chrysophyte cysts to diatom frustules ratio were coincident with logging activities in the catchment. Subsequent recreational use in the mid-20th century led to a shift from oligotrophic diatom species to disturbance indicators. An abrupt increase of diatom-inferred pH suggests higher primary productivity and increased cation concentrations due to increased in-lake-alkalinity generation. Enhanced nutrient supply from soil decomposition processes following logging and more recently from intense recreational usage during the 20th century have produced unique carbon and nitrogen isotope signatures in the sediment that have not been observed over the past ca. 1600 years.

Remarkably, the major changes observed in diatom assemblages around 1920 AD were not equally reflected in the quantitative diatom-based TP reconstructions. As fossil diatom samples integrate all seasons, this proxy reflects mean annual TP. The latter has actually been low during the last twenty years, corresponding well with the diatom-inferred values. Lake phosphorus peaks in summer, when planktonic diatoms benefiting from higher nutrient levels are dominant. During seasons when Walden Pond is less subject to recreational use (e.g., spring, autumn, and winter), the lake water returns to relatively low nutrient concentrations.

Presently the lake is in an oligo- to mesotrophic state and, since the ~ 1970s, the diatom assemblages and carbon and nitrogen stable isotope compositions have stabilized, probably as a result of effective management practices that have reduced nutrient loading. However, bacteriological decomposition of organic matter leads to oxygen-depleted conditions in the hypolimnion of the lake, which may lead to further eutrophication of Walden Pond, if no reduction of nutrient inputs is achieved. Therefore, current management strategies including monitoring of groundwater down gradient from the septic leach field, storm water-runoff control, and public awareness activities should be continued in effort to further reduce nutrient loading. Unless recreational usage is sharply curtailed, however, it seems unlikely that the current limnological status of Walden Pond will revert to pre-disturbance, oligotrophic conditions evident in the paleolimnological record.

3.9 Acknowledgements

We are grateful for the very helpful comments of the members of the Paleolimnology-Paleoecology Laboratory at Université Laval and of anonymous reviewers on earlier versions of the manuscript. We thank Susan Clayden for counting the pollen and John Smol for providing information about the chrysophytes. This study was supported by NSF and NSERC grants to D. Foster and to R. Pienitz, respectively, and by logistical support from the Centre d'études nordiques and Harvard Forest.

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4 Environmental history of two New England lakes: natural dynamics versus human impacts

4.1 Résumé

L'analyse de diatomées fossiles de deux lacs en Nouvelle-Angleterre (États-Unis) a évalué les impacts des changements climatiques et des perturbations anthropiques sur ces derniers au cours des derniers 1500 ans. Dans le Levi Pond, Vermont, un COD croissant pendant les derniers 2000 ans semble indiquer une augmentation de l'humidité, associée au refroidissement lié au Néoglacial. Suite à la déforestation des bassins versants pendant le 18e et 19e siècle, des changements importants des assemblages de diatomées et un enrichissement soit en carbone organique dissout (COD) (Levi Pond) soit en phosphore total (North Round Pond) ont été observés. Après un ouragan au North Round Pond, le COD et l'acidité ont augmenté. Malgré la récupération de la forêt au début du 20e siècle, les communautés algales n'ont pas rétabli jusqu'à aujourd'hui leur composition originale avant-perturbation dû à une récupération décalée de l'acidification et de l'enrichissement de l'eau en nutriments ainsi qu'à cause d'un développement continu de marais.

4.2 Abstract

Analyses of sedimentary diatoms in two New England ponds indicate limnological changes during the past 2500 years related to climate change, anthropogenic activities and natural disturbance. Deforestation during the 18th and 19th centuries temporarily affected diatom assemblages with subsequent recovery, but algal communities did not return to pre-settlement conditions due to natural disturbances and delayed recovery from acidification. Short-term rises in diatom-inferred dissolved organic carbon (DOC) were related to partial removal of vegetation by logging in the Levi Pond catchment and a hurricane and increased aquatic productivity at North Round Pond. At Levi Pond, increasing diatom-inferred DOC concentrations during the past ca. 2000 years seem to reflect a long-term increase of

allochthonous organic matter loading and peat development in the watershed related to moister conditions, which is supported by coincident patterns in the stable isotope, chironomid and pollen records. These results correspond to moisture patterns in adjacent areas inferred by pollen and sediment analyses, suggesting that diatoms in Levi Pond recorded a larger regional trend in increasing moisture. Our results show that long-term trends in climate change and small-scale natural disturbance patterns still influence the dynamics of anthropogenic altered ecosystems. Furthermore, this study suggests that fossil diatoms may be a promising proxy for future paleohydrological studies in temperate regions.

4.3 Introduction

Land use by European settlers, such as forest clearance, agriculture, urban and industrial development, have had a marked impact on terrestrial and aquatic ecosystems in New England, U.S.A. (Davis and Norton 1978; Engstrom et al. 1985; Foster 1995; Foster et al. 1998). Often, these impacts are described in relation to the “natural baseline conditions”, namely the ecosystem state before European arrival (Foster et al. 1998). However, there is evidence that the pre-settlement environment and vegetation were highly variable, probably related to climatic change, natural disturbances such as fire and hurricanes, and native people’s activities (Gordon 1953; Russell 1983; Gajewski 1987; Rhodes and Davis 1995; Fuller et al. 1998). Since the interaction between climate change and human disturbance may produce major changes in ecosystem structure and dynamics, it is essential to understand pre-settlement ecosystem conditions in order to assess human impact. Insight into past climatic impacts on natural systems and their interaction with human disturbance will also help predict how human-altered ecosystems will respond to future climatic change.

One major concern in studying human impacts on ecosystems is the nature and pace of recovery. Much of the historically deforested areas in the New England uplands have been abandoned and reforested in the late 19th century due to relocation of US agriculture to mid-western states and of rural populations to urban centres (Foster 1995). However, vegetation composition and lake environments have not returned to pre-settlement conditions, indicating that other disturbances, such as logging, forest diseases, hurricanes and fire suppression continue to influence the watersheds (Fuller et al. 1998; Francis and Foster 2001). Since many paleolimnological studies in New England have focussed on continued effects of human activities on lakes, there is a need for investigations assessing lake and watershed recovery after disturbance has ceased (Francis and Foster 2001).

Paleolimnological studies using fossil diatoms have been applied in a wide range of investigations to infer long-term dynamics of lakes and their watersheds (Moser et al. 1996). Diatoms, which are well preserved in lake sediments, are powerful indicators of past environmental change, such as lake trophic status (Hall and Smol 1999) and lake acidification (Batterbee et al. 1990; Cumming et al. 1994). Applications of diatoms to climatic (Smol and Cumming 2000) and hydrological studies (Moser et al. 2000) are mostly conducted in (sub-) arctic and alpine regions, at ecotonic transitions and in semiarid areas, but seldom in temperate regions. The reason for this is that paleoclimatic inferences in temperate, forested lake regions are challenging, because lakes are hydrologically open (Smol and Cumming 2000), and pH and trophic status often exert a dominating influence on diatom assemblages in the southern, more densely populated areas (Dixit et al. 1999). However, diatoms are sensitive to lake dissolved organic carbon (DOC) concentrations (Kingston and Birks 1990; Pienitz and Smol 1993; Korsman et al. 1994; Fallu and Pienitz 1999) which in turn are strongly controlled by precipitation patterns (Schindler et al. 1996). They may therefore have some potential for paleoclimatic inferences in dilute, temperate lakes. However, this has not yet been tested, presumably for the reasons discussed above.

The main question we address in this study is: Which were the driving natural and anthropogenic factors affecting the past lake environment? More specifically, we investigate the following problems: Which changes in the physical and chemical lake characteristics can be identified? How do these changes relate to natural processes and human disturbances in the watershed and in the region? How do the lakes respond to recovery of the watershed vegetation? What is the relative importance of local versus regional factors determining lake evolution? We attempt to answer these questions by reconstructing the environmental history of two New England lakes for the last ca. 2000 years through fossil diatom analyses in the context of regional vegetation dynamics and disturbance history.

4.4 Study sites

The study sites Levi Pond and North Round Pond are small oligotrophic and acidic headwater lakes with similar elevation and watershed : lake area ratio (Table 4.1). The bedrock is mainly metamorphosed Paleozoic gneiss and schist with some granitic intrusions, overlain by Wisconsin till and humus-rich organic soils (Siccama 1974). According to historical data, both lakes have undergone similar anthropogenic disturbance with logging in the watershed after European settlement and subsequent re-establishment of the vegetation.

Some differences in location, site characteristics and natural disturbance history are important for interpreting the paleolimnological record. Levi Pond, situated in the Green Mountains of Vermont (Fig. 4.1), has a greater maximum depth (6.8 m) than North Round Pond (3.4 m). However, the maximum depth of Levi Pond was measured in a deep depression in the centre of the lake, whereas most of the lake basin is shallower (ca. 3 m depth). At the western edge, a *Sphagnum* wetland of about 10 m width covers 40 % of the shoreline, including some dead tree stems (Neil Kamman, Vermont Department of Environmental Conservation, personal communication; D. Köster, personal observation). While both lakes are surrounded by northern hardwood-conifer forest, there is a distinctive *Picea* population close to the shore of Levi Pond, all around the lake. Levi Pond is more acidic and has lower nutrient concentrations than North Round Pond (Table 4.1). Major logging around Levi Pond was recorded in the mid-1800s, and the watershed was used shortly for sheep pasture. Afterwards, moderate logging in the watershed continued until ca. 1950. Near the end of the 1970s, the natural fish fauna was destroyed by rotenone application in order to stock trout for fishing.

The Pisgah State Park, New Hampshire, where the watershed of North Round Pond is situated, experienced episodic logging activity after 1750 AD, but no housing or farming (Branch et al. 1930). However, for the watershed of North Round Pond, only some cutting in the early 1900s is documented (Foster 1988). In 1938, a hurricane damaged the watershed vegetation. About half of the catchment was moderately affected, and ca. 25% severely damaged (Foster 1988).

Table 4.1 Lake and watershed characteristics of the study sites.
Alkalinity, total phosphorus (TP), sulphate (SO_4) and pH data for North Round Pond are ranges from three measurements taken in February 1993 and August 1992 and chlorophyll a (Chl *a*) is one value measured in August 1992. Alkalinity, pH and sulphate data for Levi Pond are ranges for several measurements from different seasons taken each year from 1981 to 1989 and in 1999. TP for Levi Pond is the range of six measurements of spring TP taken from 1987-2003. n. d. no data. The data for North Round Pond were provided by the Watershed Management Bureau, New Hampshire Department of Environmental Sciences (Robert Estabrook) and the data for Levi Pond were provided by the Water Quality Division of the Vermont Department of Environmental Conservation, Waterbury (Neil Kamman).

	Levi Pond	North Round Pond
Town	Groton	Winchester
State	Vermont	New Hampshire
Latitude	44° 15.6' N	42° 50.8’ N
Longitude	72° 13.4' W	72° 27.2’ W
Elevation (m.a.s.l.)	501	317
Lake surface area (ha)	9	4.3
Watershed area (ha)	57	21.3
Watershed:lake are ratio	6:1	5:1
Maximum depth	6.8	3.4
pH	4.9-5.6	5.7-6.1
Alkalinity (µeq l^{-1})	-0.2-1.6	20-44
TP (µg l^{-1})	7-11	10-14
SO_4^{2-} (mg l^{-1})	3.9-7.8	3-4
Chl *a* (µg l^{-1})	n.d.	3.9
Coring date	11 Nov. 1994	20 Feb. 1997

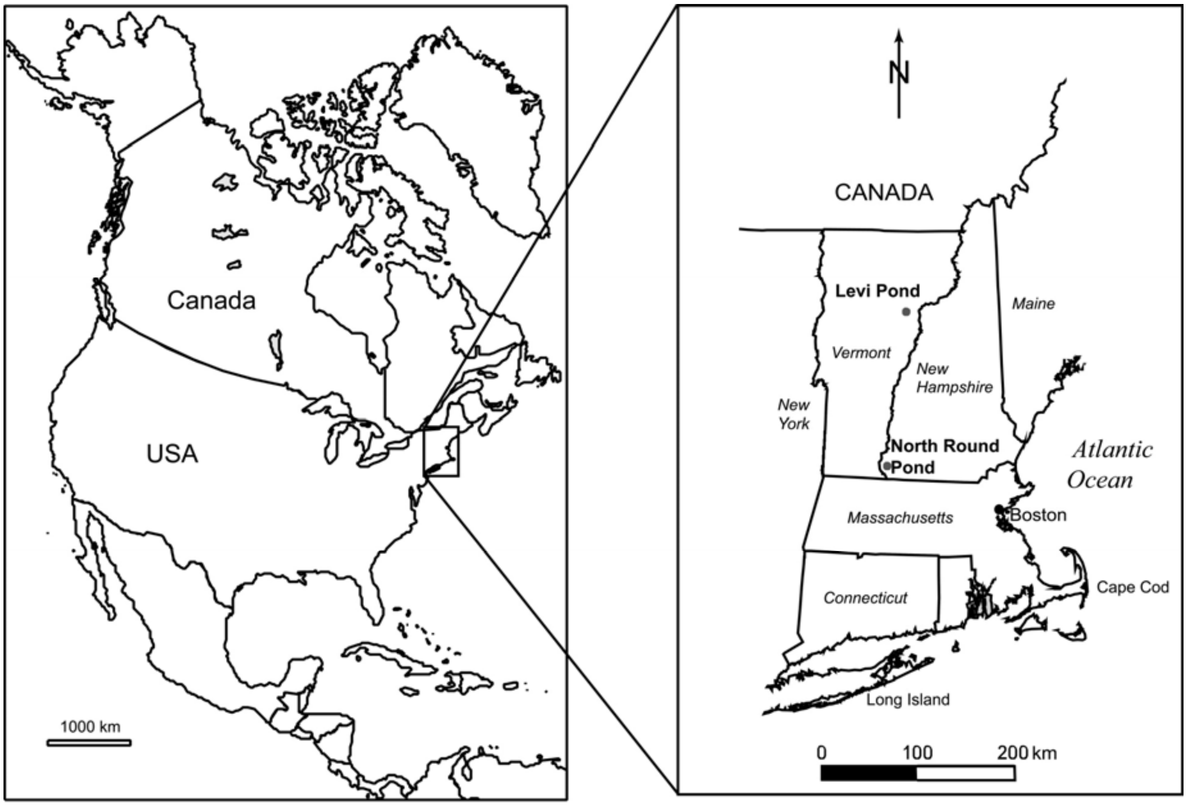

Figure 12 Map of the study region and location of Levi Pond and North Round Pond in New England.

In the undamaged part, several old growth forest stands are preserved (Foster 1988). A lake survey in 1950 stated that the shoreline was 100% forested (Bob Estabrook, New Hampshire Department of Environmental Services, Concord).

4.5 Methods

Sediment cores of 1.15 m (North Round Pond) and 1.02 m (Levi Pond) length were taken at the deepest point of the lakes using a clear Lexan coring tube fitted with a rubber piston. The sediment cores were sub-sampled at 1 cm intervals and stored at 4°C.

Bulk sediment samples of 1 cm (Levi Pond) and 4 cm (North Round Pond) thickness were radiocarbon dated by accelerated mass spectroscopy at Beta Analytic Laboratories, Miami, Florida. Radiocarbon dates (^{14}C yr BP) were calibrated (cal. yr BP) using the computer program CALIB version 4.3 (Stuiver and Reimer 1993) and converted to calendar years (yr AD) by adding 50 years in order to permit consistent discussion of paleolimnological data in the historical context (Table 4.2). As the dates for North Round Pond did not form a linear curve, the error range was used to assign the date that had the best fit using a linear function of age versus depth (Table 4.2). For Levi Pond, the calibrated dates were used without manipulation. The recent chronology was established by the ^{210}Pb technique and ages were calculated using a CRS point transformation model (Binford 1990). The settlement horizon for North Round Pond was based on the rise of agriculture indicator pollen, such as *Ambrosia* and *Rumex*, and was assigned to the date of establishment of the town of Winchester in 1733 AD. Linear interpolations were made between the ^{14}C dates, the settlement date and the oldest ^{210}Pb date (Fig. 4.1).

Organic matter was measured at 1 cm intervals using standard loss-on-ignition procedures at 550°C (Dean 1974).

Diatom extraction followed standard strong-acid-digestion techniques (Pienitz et al. 1995), and a minimum of 500 valves per slide were enumerated under 1000x magnification. Species were identified according to standard and regional taxonomic references (Krammer and Lange-Bertalot 1986-1991; Camburn and Charles 2000; Fallu et al. 2000). The fossil assemblages were subdivided into diatom zones by optimal partitioning using the computer program ZONE (S. Juggins, unpublished program) and the number of significant zones was estimated by the broken-stick model (Bennett 1996).

Quantitative reconstructions of environmental variables and calculation of associated sample-specific reconstruction errors were carried out using the computer program C^2 (Steve Juggins, unpublished program). The pH model using weighted averaging (WA) with inverse deshrinking and the total phosphorus model using Gaussian logit regression (GLR) were based on a calibration set including 82 New England lakes (Köster et al. chapter 2), which were selected from a larger calibration set (Dixit et al. 1999) in order to limit its geographical extent to that of the paleolimnological study sites. For dissolved organic carbon (DOC) reconstructions, a model encompassing 58 lakes situated along a latitudinal transect from the boreal forest to the tundra in northern Quebec was applied (Fallu and Pienitz 1999). Errors for quantitative inferences were estimated by bootstrapping.

For detecting major trends in the fossil diatom assemblages, principal components analysis (PCA) with inter-sample distance scaling and covariance matrix was carried out on species percentage data using the computer program CANOCO for Windows, version 4.0 (ter Braak and Šmilauer 1998).

In order to assess the reliability of quantitative reconstructions, the fit of the fossil samples to the variables of interest were estimated by comparing the squared residual distances of the modern and fossil samples to the first axis in a canonical correspondence analysis (CCA) which was constrained to the respective variable. Fossil samples with a residual distance equal or larger than the residual distance of the extreme 5% (or outside the 95% confidence interval) of the modern training set samples are considered to have "very poor" fit to the variable, those with values equal or larger than the extreme 10% have "poor fit", and all other samples have a good fit (Birks et al. 1990).

4.6 Results

4.6.1 Chronology and sedimentology

Radiocarbon ages for both cores are reported in Table 4.2 and the overall chronologies are plotted in Fig. 4.2.

The LOI profile of Levi Pond showed two minima at the core bottom around 70 cm depth (ca. 270 BC) with 33% and around 56-58 cm (0 AD) with 38% (Fig. 4d). Afterwards, the organic matter in the sediments increased until 48% at 45 cm (ca. 400 AD), remained stable until 28 cm (ca. 1200 AD) and started to decrease above 28 cm. From 10 cm to the top of the core (1920 -1994 AD) it remained relatively stable.

Table 4.2 Calibrated radiocarbon dates for Levi Pond and North Round Pond, USA. Dating was performed on bulk sediment samples at Beta Analytic, Miami, Florida. Ages for North Round Pond were assigned to the date that best fitted a linear function through the four age ranges.

	Depth (cm)	Lab. number	Age ^{14}C yr BP	Age cal. yr BP	Assigned age (best fit)	Age yr BC/AD
Levi Pond	29-30	AA 35307	1100	1010 ± 80	1010	1040
	45-46	AA 35308	1740	1640 ± 100	1640	410
	59-60	AA 35309	2150	2090 ± 100	2090	-40
	79-80	AA 35310	2415	2420 ± 50	2420	-370
North Round Pond	44-48	n.a.	570	520-740	640	1310
	65-69	n.a.	1000	990-1170	990	960
	91-95	n.a.	1570	1410-1630	1410	540
	116-120	n.a.	1650	1540-1740	1740	210

n.a. = not available

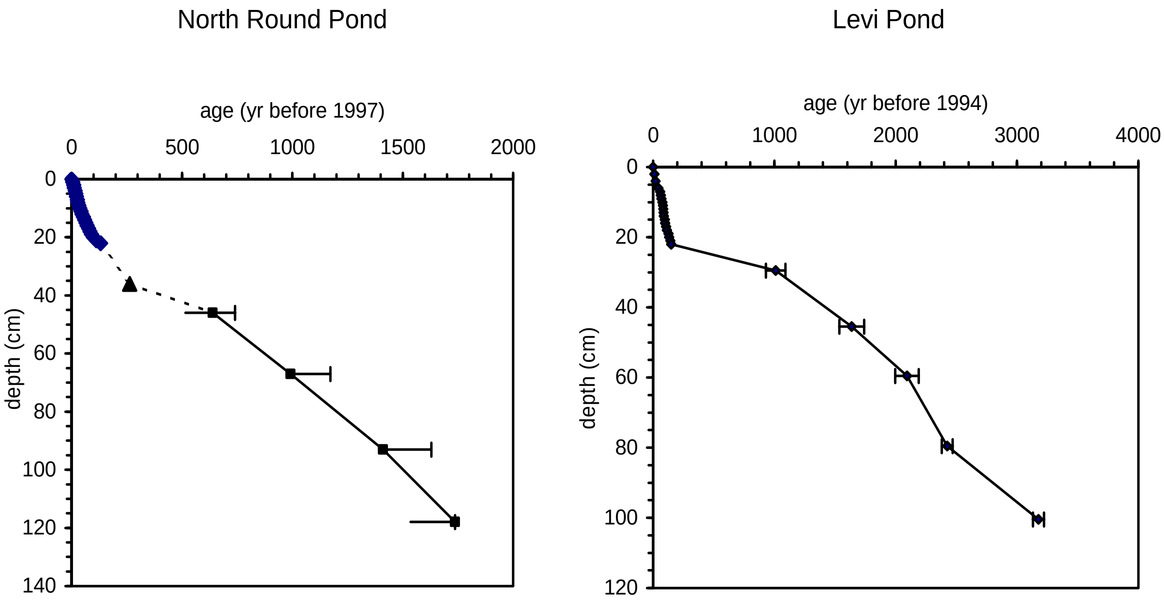

Figure 13 Age-depth curves for a) Levi Pond and *b) North Round Pond using ^{210}Pb and ^{14}C methods as well as the settlement horizon based on pollen agriculture indicators.
50 years were added to the calibrated ^{14}C dates in order to fit with ^{210}Pb dates. See Figs. A.2 and A.3 in the appendix for detailed ^{210}Pb results. * modified from Francis and Foster (2001).

In contrast to Levi Pond, organic matter content in North Round Pond sediments increased more steadily from 40% at 80 cm (ca. 750 AD) to 50% at 60 cm (1100 AD; Fig. 4.6 e). Afterwards, it decreased rapidly to 42% at around 1200 AD, remaining low afterwards, until a second increase to 50% occurred around 40 cm (1750 AD). The largest increase from 40% to ca. 55% occurred in the upper 20 cm (ca. 1920 AD to the present; Fig. 4.6 e).

4.6.2 Diatom assemblages and quantitative reconstructions

4.6.2.1 Levi Pond

Four significant zones with different diatom assemblages were identified in the sediment core from Levi Pond (Fig. 4.3). Diatom assemblages in zone I consisted mainly of *Tabellaria flocculosa* (Roth) Kützing str. IIIp sensu Koppen, *Pinnularia mesolepta* (Ehrenberg) W. Smith, *Brachysira brebissonii* Ross in Hartley, *Cymbella hebridica* (Grunow) Cleve, *Navicula subtilissima* Cleve, and *Navicula heimansii* van Dam and Kooyman, which have been observed in New England mainly in acidic, oligotrophic waters (Davis et al. 1994b; Dixit et al. 1999).

In zone II, from 54 cm (ca. 100 AD) on, *Aulacoseira distans* var. *distans* (Ehrenberg) Simonsen increased from around 5 % to around 15 % relative abundance. At the same time, *Brachysira brebissonii*, *Navicula modica* Hustedt, *Navicula mediocris* Krasske, and *Nitzschia perminuta* (Grunow) M. Paragallo decreased slightly, whereas *Eunotia hemicyclus* (Ehrenberg) Ralfs started to appear more commonly.

With the start of the third zone at 30 cm (ca. 1000 yr AD), Aulacoseira distans var. distans increased further to around 20 %, simultaneously with an important increase of Eunotia hemicyclus by ca. 10 %, and a small, but abrupt decrease of Pinnularia interrupta W. Smith. Melosira arentii (Kolbe) Nagumo & Kobayasi temporarily became a dominant part of the assemblage from ca. 1800 to ca. 1959 AD, coincident with the appearance of settlement indicators in the pollen profile (S. Clayden and J. McLaughlin, Harvard Forest, unpublished data). This change is also recorded by the sample scores on PCA axis 2 (Fig.3).

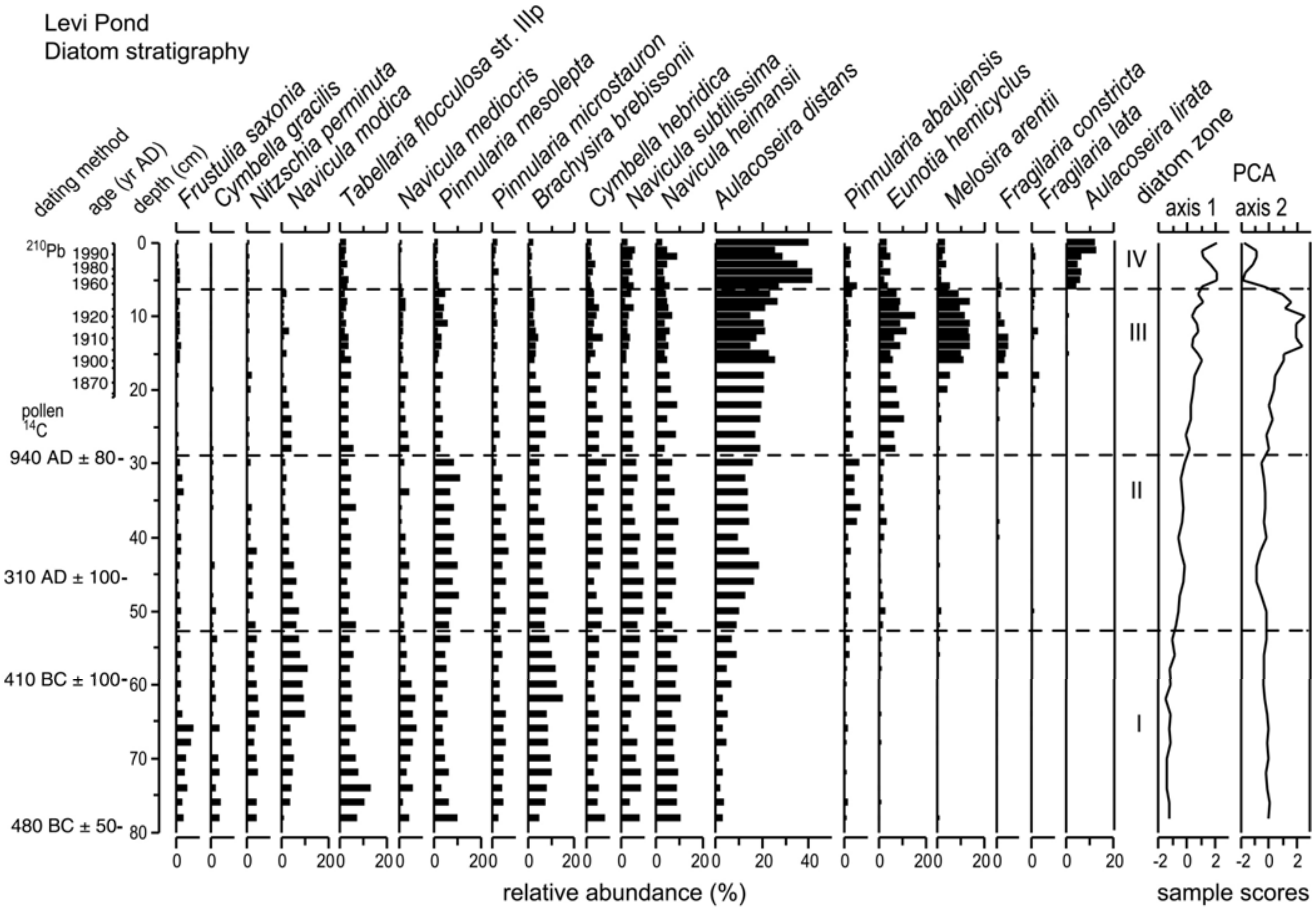

Figure 14 Diatom stratigraphy of Levi Pond with major zonation and fossil sample scores on PCA axes 1 and 2. Diatom taxa are arranged by their chronological appearance in the sediment sequence.

In the most recent sediments, from 7 cm to 0 cm (ca. 1940 yr AD to 1997 yr AD), *Melosira arentii* and *Eunotia hemicyclus* declined whereas *Aulacoseira lirata* (Ehrenberg) Ross increased from almost 0 to 10 %, and *Aulacoseira distans* var. *distans* reached maximum abundances of 40%.

These small-scale changes form together a long-term trend in diatom assemblages starting at ca. 100 yr AD and continuing until the present, indicated by a gradual increase in fossil sample scores on PCA axis 1 (Fig. 4.3). This trend corresponds both to increasing proportions of planktonic or tychoplanktonic (centric) diatoms (e.g. *Melosira arentii*, *Aulacoseira* spp.) at the expense of benthic (pennate) diatoms (e.g. *Navicula* spp., *Pinnularia* spp.) (Fig. 4.4 a) and increased diatom-inferred DOC values (Fig. 4.4 b). This development also coincides with a gradual increase of *Picea* pollen (Fig. 4.4 c), and to changes in bulk organic stable isotopes, such as decreasing $\delta\ ^{13}C$ and increasing $\delta\ ^{15}N$ (Brent Wolfe, personal communication).

The CCA with modern and fossil samples showed that the fossil assemblages have variable fit to the DOC model (Fig. 4.4 b). Almost half of the samples (22) have good fit to DOC, 8 levels have poor and 17 samples have very poor fit, indicating that reconstructions for the latter samples are less reliable. However, several samples with good fit were present in each diatom zone, suggesting that the model is appropriate for reconstructing major trends in DOC concentrations of Levi Pond. As almost all fossil samples from Levi Pond show a very poor fit to both the pH and the TP model (data not shown), we do not present the inferences derived from these models.

4.6.2.2 North Round Pond (New Hampshire)

Diatom assemblages in North Round Pond were dominated by oligotrophic to mesotrophic species throughout the last ca. 1500 years (Fig. 4.5), which is also indicated by diatom-inferred TP values between 10 and 15 $\mu g\ l^{-1}$ (Fig. 4.6 d). Cluster analysis allowed to distinguish three significant changes in the fossil diatom assemblages as detailed below.

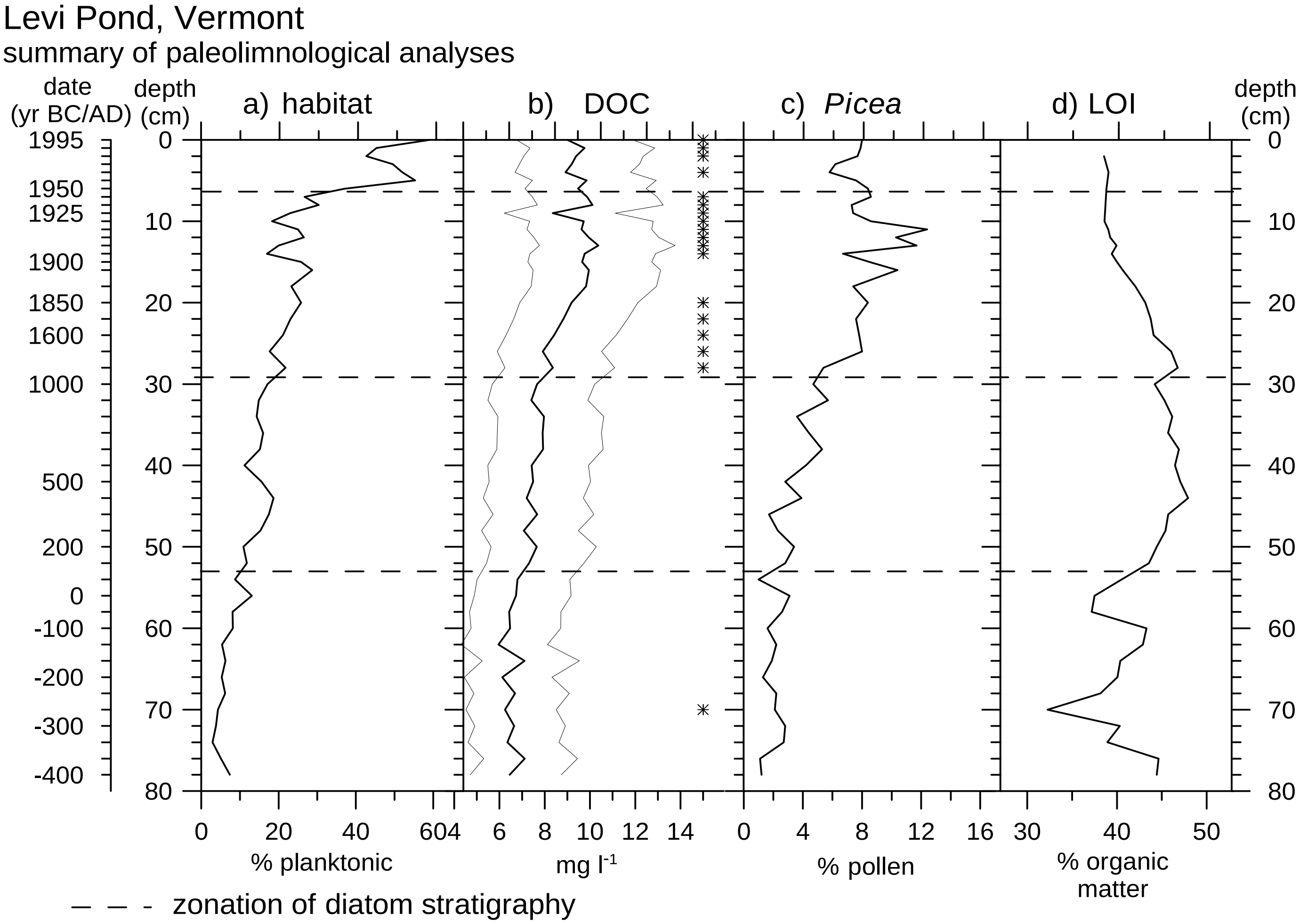

Figure 15 Summary of paleolimnological analyses for Levi Pond. a) percentage of planktonic diatom taxa, b) diatom-inferred DOC, c) relative abundance of *Picea* pollen, d) percent organic matter as estimated by LOI.

* = samples with very poor fit to DOC indicating unreliable value. Fine lines in b indicate error ranges for quantitative inferences estimated by bootstrapping.

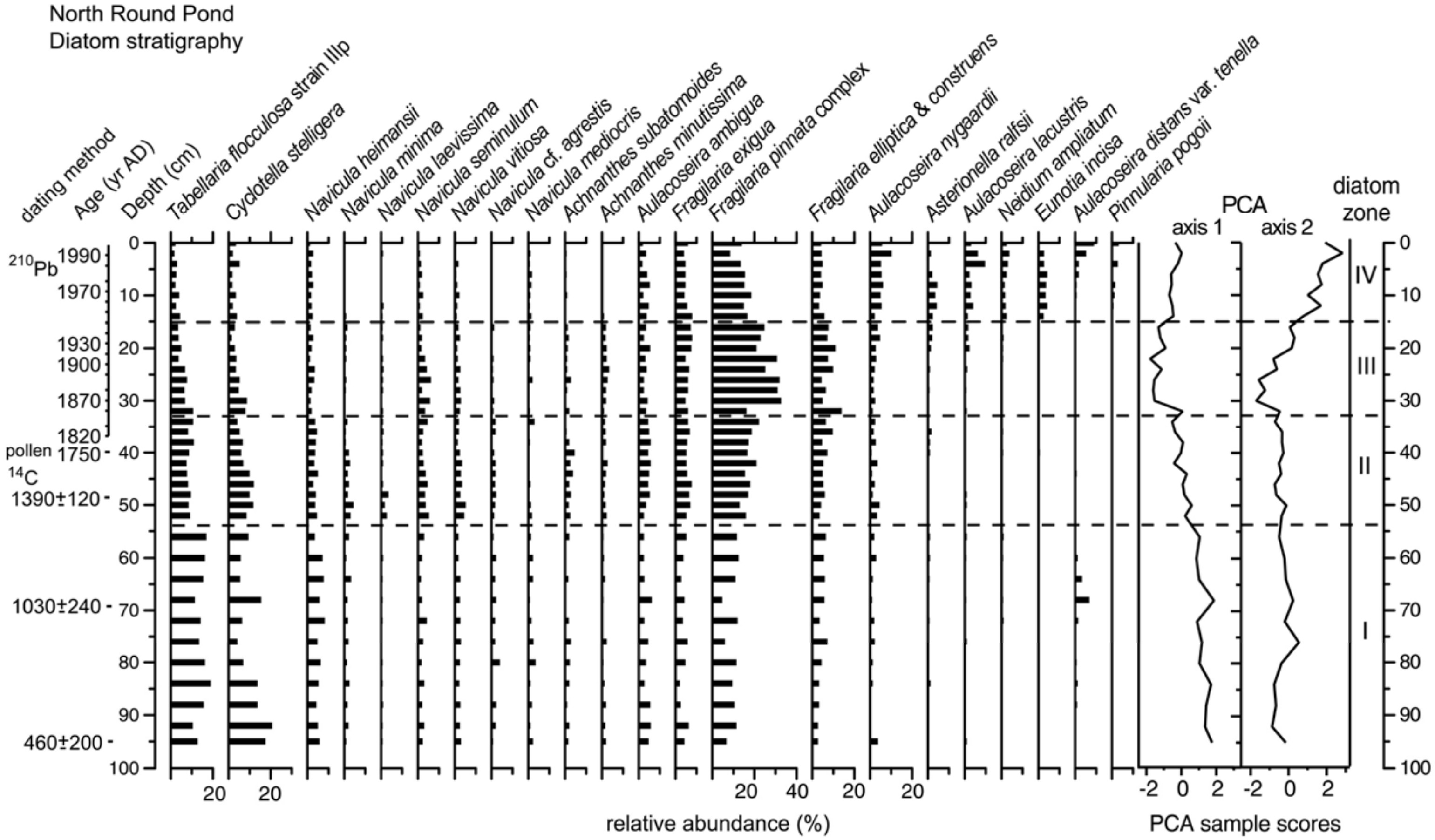

Figure 16 Diatom stratigraphy of North Round Pond with major zonation and fossil sample scores on PCA axes 1 and 2.

In the first zone (95 cm – 56 cm; ca. 450 – 1300 AD), diatom assemblages were dominated by *Tabellaria flocculosa* str. IIIp, *Cyclotella stelligera* Cleve and Grunow, *Fragilaria pinnata* Ehrenberg, and *Navicula heimansii*. With the beginning of zone II at 52 cm (ca. 1300 AD), benthic species (*Fragilaria* spp. and *Navicula* spp.) increased at the expense of planktonic species (*Cyclotella stelligera* and *Tabellaria flocculosa* str. IIIp). The diatom-inferred pH (Fig. 4.6 c) and TP (Fig. 4.6 d) increased slightly. These changes coincided with an increase of the charcoal-pollen ratio as well as a modification of regional vegetation, indicated by an increase of chestnut (C*astanea*) pollen and a decrease of hemlock (*Tsuga*) and beech (*Fagus*) (Francis and Foster 2001). At 32 cm (ca. 1800 AD, Zone III), *Fragilaria* spp. abundance increased further, coincident with a decrease of organic matter (Fig. 4.6 e) and an increase of aquatic macrophyte pollen (Francis and Foster 2001). During the most recent period (14-0 cm; ca. 1940-1997 AD; Zone IV) several acidophilic taxa (*Eunotia* spp., *Aulacoseira* spp.) appeared or increased in abundance. Diatom-inferred pH decreased (Fig. 4.6 c) and diatom-inferred DOC increased (Fig. 4.6 b), coincident with the increase of organic matter in the sediments (Fig. 4.6 e).

The good fit of the fossil diatom samples at North Round Pond to DOC, with the exception of two levels with poor fit (0, 2 cm), suggests that the quantitative DOC inferences are reliable (Fig. 4.6 b). Although the DOC rise was within the bootstrapped reconstruction errors, the consistent increasing trend to the core top and the increase of indicators for high DOC (e.g., *Aulacoseira lacustris* (Grunow) Krammer, *Eunotia incisa* Gregory) suggest that DOC or a close correlate (such as light availability) has at least partly driven the diatom assemblage change.

Most fossil samples of North Round Pond have good fit to pH and TP, except levels 16-20 and 34-36 cm, which have poor fit to pH and TP (data not shown), and the samples 22 to 32 cm, which are outside the 95% confidence interval of the model variation (Figs. 4.7 c and d).

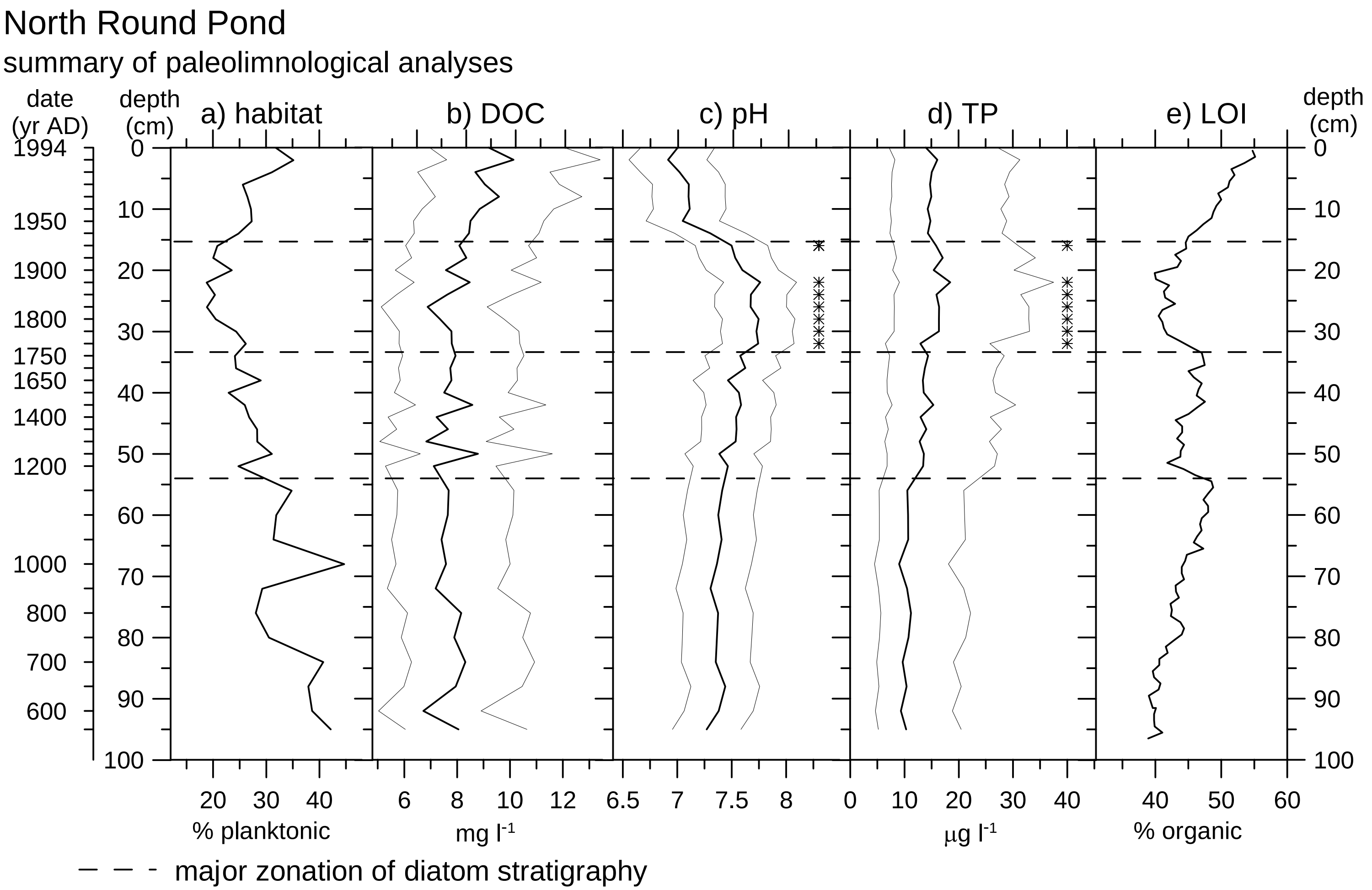

Figure 17 Summary of paleolimnological analyses for North Round Pond. a) percentage of planktonic diatom taxa, b) diatom-inferred DOC, c) diatom-inferred pH, d) diatom-inferred total phosphorus (TP), d) percent organic matter as estimated by LOI.
* = samples with very poor fit to the reconstructed variable indicating unreliable value. Fine lines in b, c, and d indicate error ranges for quantitative inferences estimated by bootstrapping.

4.7 Discussion

4.7.1 Levi Pond

Although the fossil species composition (Fig. 4.3) indicates that Levi Pond has been slightly acidic and oligotrophic throughout the past 2400 years, large changes in diatom assemblages suggest that the lake has not been a stable system during that time.

The overall long-term trend of diatom assemblages during the last ca. 2000 years with increased ratios of planktonic to benthic species and higher DI-DOC suggest that relative availability of pelagic habitats and/or lake DOC increased. The planktonic/benthic species ratio mainly reflects the increasing relative abundance of *Aulacoseira distans* var. *distans* and, in the upper levels, *Aulacoseira lirata*. These algae are heavily silicified tychoplanktonic species, which need water turbulence and/or high water levels for suspension in the water column. Therefore, the increased abundance of *Aulacoseira* spp. from 0 yrs AD on may indicate increased mixing intensity or lake level. Given the continuously closed forest vegetation around the pond before European settlement, as indicated by the dominance of tree species throughout the pollen sequence (Harvard Forest, unpublished data), water mixing by wind is unlikely to have changed before 1800 AD. However, water levels may have increased due to a continuing positive water balance, for example caused by increasing precipitation and/or reduced evaporation. Independent indicators for lake levels, such as macrofossil analyses, would be necessary to test this hypothesis.

The close correlation of the quantitative DOC reconstructions for Levi Pond with the first PCA axis suggests that the long-term species changes observed in the stratigraphy reflect changes in DOC concentrations. Coloured substances contained in DOC are largely responsible for the attenuation of photosynthetic available radiation (PAR) (Wetzel 2001) and ultraviolet radiation (UV-A and UV-B) in lakes (Morris et al. 1995), thereby controlling the light conditions for phytoplankton assemblages (Williamson et al. 1996). Therefore, the structure of diatom assemblages may have been altered by changing underwater light conditions due to increased DOC concentrations.

It may be possible that the dominant species *Aulacoseira distans* solely drives the DOC reconstructions and that this was mainly caused by increased pelagic habitat availability. This hypothesis is rejected by parallel increases of several other species with high DOC optima (*Eunotia hemicyclus, Pinnularia abaujensis* (Pantocsek) Ross, *Melosira arentii*) and declines of low DOC indicators (*Pinnularia microstauron* (Ehrenberg) Cleve, *Navicula mediocris, Nitzschia perminuta*) (Fallu and Pienitz 1999; Camburn and Charles 2000).

As the DOC increase in the second site of our study, North Round Pond, occurs parallel to a decline in pH, the question arises if the diatoms in Levi Pond also respond to a change in acidity. In the modern calibration set, DOC is not correlated with pH ($r = -0.27$) (Fallu 1998), indicating an independent response of diatoms to DOC. Like in Levi Pond, Korsman et al. (1994) have shown in several Swedish lakes that diatom-inferred DOC may increase due to catchment vegetation changes without parallel acidification. Measured pH at Levi Pond during the 1980s was around 5.5 and high SO_4 concentrations (maximum 7.8 mg l^{-1} in February 1981) suggest that Levi Pond has been subject to contamination by atmospheric deposition (Neil Kamman, Vermont state). As our diatom-based pH reconstructions were not reliable because of poor fit, another model would be needed to test the hypothesis of recent acidification in Levi Pond.

Within-lake variations in DOC are mainly controlled by climatic processes (Pace and Cole 2002). Higher DOC concentrations can be produced by late ice-out and higher precipitation (Pace and Cole 2002), longer residence times (Curtis and Schindler 1997), and peat development in the catchment (Dillon and Molot 1997). *Aulacoseira distans* var. *distans* has been associated with higher DOC concentrations due to peatland development in a Minnesota bog (Brugam and Swain 2000). The residual tree stems in the *Sphagnum* wetland on Levi Pond's shore indicate that it has developed recently. A stratigraphic analysis of the shore sediments and/or macrofossil analysis of the lake sediments would be necessary to test the hypothesis that this wetland has developed during the last 2000 years. The timing of ice-out is determined by winter air temperature (Assel and Robertson 1995), therefore colder winter temperatures might have delayed ice-out and increased DOC in Levi Pond. Climate reconstructions for the north-eastern United States using pollen transfer functions indicated a trend to moister and/or cooler conditions starting at ca. 2000 years BP (Gajewski 1988). Additional independent evidence for a cooler and/or moister climate during the last 2000 years at Levi Pond is provided by pollen, chironomid and stable isotope analyses, as discussed below.

The broad correspondence of the long-term trend in diatoms with increased *Picea* (spruce) pollen abundances (Fig. 4.4 c) suggests that one factor controlled, directly or indirectly, both the terrestrial and the aquatic ecosystem. Korsman et al. (1994) showed that *Picea* immigration to some Swedish watersheds led to increased diatom-inferred lake DOC, probably due to increased accumulation of humus. In north-eastern North America, spruce prefers moist and cool conditions (Webb et al. 1993). The increase of *Picea* pollen has been related to cooler and/or wetter conditions in Michigan lakes from the 13th century on (Bernabo 1981), in southern Ontario starting at ca. 600 yr BP (Campbell and McAndrews 1991) and in Maine starting at ca. 1000 yr BP (Gajewski 1987). Richard (1994) argued that the widespread increase of *Picea* throughout southern Québec resulted from a greater abundance of populations on mesic sites, such as lake shores. This scenario has likely taken place at Levi Pond, where *Picea* is growing mainly close to the wetland-covered shore. Stable isotope analyses of Levi Pond sediments showed coincident decreasing $\delta^{13}C$ org values and increasing $\delta^{15}N$ org values (Brent Wolfe, unpublished data), which may indicate enhanced soil organic matter decomposition, generation and leaching due to moister conditions (Wolfe et al. 1999, 2003). The increase in relative abundances of the cool water chironomid fossils belonging to the genus *Microtendipes* from ca. 200 to 1800 AD (Donna Francis, personal communication) suggests that the increased effective humidity was, at least in part, caused by a decline in temperature.

A change to moister conditions around 2000 years ago at Levi Pond is consistent with sedimentary and pollen evidence for moister conditions during the last 2000 to 4000 years in New England (Almquist et al. 2001; Shuman et al. 2001), Ontario (Yu et al. 1997) and southern Québec (Lavoie and Richard 2000), which followed a dry spell during the mid-Holocene and corresponds to the Neoglacial cooling period. The correlation of multiple independent proxies in Levi Pond with regional evidence supports the hypothesis that the watershed of Levi Pond has undergone a long-term trend to moister conditions over the last ca. 2000 years, thereby responding to a larger regional moisture trend.

Increasing DOC concentrations and higher lake level have possibly occurred in parallel at Levi Pond, because they have the same causes and influence each other. As discussed above, both trends can result from increased moisture in the watershed. The observed relative increase of planktonic taxa may be due to higher water levels or lower water transparency caused by increased DOC, which deteriorates the light conditions for aquatic macrophytes and thereby reduces the surface for epiphytic diatoms. In return, higher water levels provide more pelagic habitat and alongside lead to increased decomposition of submerged lake shore vegetation and eventually to peat development, thereby enhancing the release of organic matter into the lake. Based on our analyses, we can conclude that there was an increase in DOC concentrations in Levi Pond, which may have been partly enhanced by higher water levels.

The change in assemblage composition between ca. 1800 and 1940 AD likely reflects historical logging and agricultural practices in the drainage basin. As the dominant diatom *Eunotia hemicyclus* is usually found in oligotrophic and dystrophic waters (Krammer and Lange-Bertalot 1991; Camburn and Charles 2000) and *Melosira arentii* in dystrophic and mesotrophic environments (Krammer and Lange-Bertalot 1991), we conclude that the disturbance was not strong enough to increase the nutrient concentrations of the lake. However, both species are indicators of high DOC concentrations and the accelerated increase in diatom-inferred DOC (Fig. 4.4 b) indicates that the lake has temporarily received higher inputs of dissolved organic carbon. Logging in the catchment of lakes can result in increased DOC concentrations due to increased erosion of humic rich soil layers (Carignan et al. 2000; France et al. 2000). Therefore it is likely that the short-term change in diatoms reflects an additional input of DOC to the lake caused by logging activities in the watershed, which accelerated the long-term, moisture-driven DOC increase.

While the diatom assemblages partly recovered from human disturbance, the overall species composition, diatom-inferred DOC, and the stable isotopes in Levi Pond sediments have not returned to pre-disturbance conditions. *Melosira arentii*, which increased most evidently after logging in the watershed, decreased around 1950 AD, indicating rapid recovery of diatom assemblages following reforestation. Conversely, the diatom *Aulacoseira distans*, which had responded to moisture balance change in pre-settlement times, continued to dominate the assemblages until 1994. In addition, the stable isotopes of carbon and nitrogen continue their decreasing or increasing trend, respectively (Brent Wolfe, unpublished data), indicating that the lake and watershed continue to be controlled by climatic factors. The reason for the recent appearance of *Aulacoseira lirata* remains unknown, but continued peat development, rising lake levels or a change in food-chain structure due to fish removal in the 1970s may have caused an increase of this species.

4.7.2 North Round Pond

The first change in diatom assemblages around 1200 AD to more benthic species (Fig. 4.6 a) correlates with declines of *Tsuga* and *Fagus* pollen, increased *Castanea* pollen, a higher charcoal-pollen ratio, and a temporal increase of the chironomid taxon *Microtendipes* (Francis and Foster 2001), as well as reduced content of organic matter in the sediment (Fig. 4.6 e). The increased charcoal content indicates higher fire frequency or intensity, which is consistent with the increased inorganic matter content in the sediments. The same vegetation and charcoal-pollen ratio changes were observed at ca. 1400-1500 AD in pollen records from several Massachusetts ponds (Fuller et al. 1998), but it remains unclear whether these patterns were due to climatic factors, fire frequency and/or Native American activities (Fuller et al. 1998). Another such event was observed around 500 AD in a wetland and lake in central Massachusetts, coincident with evidence of higher moisture availability, but uncertainties persist in terms of causal connections (Foster et al. 2002). The higher abundance of *Microtendipes* in the chironomid assemblages indicate a slight temperature decrease from ca. 1300 AD on and lasting until ca. 1870 AD. However, more independent evidence is needed to test the hypothesis that climate change has driven the changes at North Round Pond around 1300 AD.

The second change in diatom assemblages during the 19th century probably reflects logging activities in the watershed, but may also be related to natural disturbance such as fire. Although logging was a common activity in the region since settlement in the 18th century, historical evidence for logging in the North Round Pond watershed exists only for the early 20th century. The increase in the proportion of benthic species indicates a higher availability of benthic habitats (Fig. 4.6 a). The parallel appearance of aquatic macrophytes in the pollen profile (Francis and Foster 2001) provides evidence for higher surface areas on submerged macrophytes for the attachment of benthic diatoms.

As most of the change in benthic/planktonic species is represented by small *Fragilaria* species, particularly *F. pinnata*, the explanation for this assemblage change may be found in ecological preferences of this taxon. As this species is a cosmopolitan and an ecological generalist (Krammer and Lange-Bertalot 1991), the interpretation of its dominance is challenging. It has been reported to live on sand and under low-light regime in frequently river-flushed lakes (Roland Hall, personal communication). Material transported to the lake from eroded areas of the watershed following forest disturbance may have supplied that habitat and increased turbidity. The taxon has also been described as a pioneer species, which rapidly colonizes newly formed or isolated lake basins, which has often been attributed to high initial supplies of alkalinity from unweathered catchment soils and tills (Stabell 1985; Marciniak 1986; Pienitz et al. 1991; Saulnier-Talbot and Pienitz 2001). Increasing alkalinity may have resulted from enhanced erosion of catchment soils following disturbance, also indicated by a slight rise of the diatom-inferred pH (Fig. 4.6 c). Similar changes of small *Fragilaria* species have been observed in Ontario lakes following hemlock (*Tsuga*) decline during the mid-Holocene (Hall and Smol 1993), indicating that different forest disturbances may have comparable effects on diatom communities. In summary, the increased *Fragilaria* spp. abundances from ca. 1850 AD to 1940 AD seem to result from higher macrophyte abundance or an augmented input of allochthonous material, which may have caused lower transparency, higher alkalinity, and increased epipsammic habitat availability due to enhanced runoff from deforested areas. However, the relative importance of these factors remains unknown.

After ca. 1940, the most important shift in diatom assemblage composition indicates a major disturbance in the watershed. The increase of acidophilic taxa, such as *Asterionella ralfsii* W. Smith and *Neidium ampliatum* (Ehrenberg) Krammer, and the resulting decline in diatom-inferred pH suggest that the lake has undergone acidification, accompanied by a small increase in diatom-inferred DOC. One possible cause of lake acidification is atmospheric deposition ("acid rain") during industrial development. Deposition of materials associated with fossil fuel combustion started in the late 1800s and early 1900s (Charles 1990) and acidification of New England lakes began in the early to mid 20th century (Davis et al. 1994a), coincident with the limnological changes seen in North Round Pond.

Acidification was probably enhanced by the destruction of large parts of the watershed vegetation by a major hurricane the 20th of September 1938 (Foster 1988). Opening of the forest vegetation may have enhanced leaching of organic and inorganic acids from the soils into surface waters. Additionally, an abrupt decrease in $\delta^{18}O$ indicates a flush of precipitation input, likely representing enhanced snowmelt during the springs following the hurricane (Brent Wolfe, personal communication). As snow is naturally acidic, rapid input of acidic melt water may also have favored acidophilic taxa.

The acidification effects and the increasing trend in DOC and sedimentary organic matter last until the surface of the core, indicating that the lake ecosystem has not fully recovered since human disturbance ended and reforestation after the hurricane. Controls of SO_2 emissions implemented in the USA after the amendments in 1970 to the Clean-Air-Act have resulted in decreased atmospheric sulfur concentrations, but minimal changes were achieved in NOx emissions (Driscoll et al. 2001). Delayed recovery from acidification due to acidified watersheds has been observed in several regions of eastern North America (Stoddard et al. 1999). Delaying processes include decreased acid neutralizing capacity (ANC) of the soils by reduced base cation concentrations (Likens et al. 1996) and increased N and S concentrations, which easily leach acids into surface waters (Aber et al. 1998; Driscoll et al. 1998). These processes may have played a role in delaying the recovery from acidification at North Round Pond.

The reason why DOC and sedimentary organic matter did not return to pre-disturbance levels in, as should be expected from the totally reforested watershed, may be increased aquatic productivity as suggested by Francis and Foster (2001). They argued that decreasing C/N ratios, higher macrophyte pollen and spore abundance and the appearance of eutrophication indicators in the chironomid assemblages in the post-settlement period of North Round Pond may be attributed to increased nutrient inputs from the watershed, increased sedimentation rate and filling of the lake basin. However, the sedimentary and chironomid changes occurred ca. 1930 AD, i.e. showed a delayed response by ca. 100 years compared to the appearance of macrophytes. This indicates that different factors have driven these changes or that chironomids responded with a significant time lag. The diatom assemblages indicated limnological changes at North Round Pond with similar timing but of different nature. Diatoms did reflect a slight nutrient change at the time of macrophyte increase, but also increased habitat availability which may be linked to the rise in aquatic macrophytes. Similar to the results in our study, Francis and Foster (2001) observed most changes in chironomid assemblages after 1930 AD, when logging in the watershed was recorded and a big hurricane affected the watershed. They interpreted these recent changes as a lack of recovery from the effects of earlier deforestation or as a response to other confounding disturbance factors. These other disturbances (acidification and increased DOC concentrations following a major hurricane) were identified and interpreted in more detail in the present study. This indicates the value of combining multiple proxies to infer past changes in environmental conditions.

4.7.3 Diatoms, DOC and climate in temperate lakes

Diatoms appeared to respond sensitively to changes in lake DOC concentrations which in turn are coupled to climate-driven moisture balance and natural or anthropogenic forest disturbance. In both lakes, rising diatom-inferred DOC was related to partial removal of vegetation by logging or the effects of a hurricane. At Levi Pond, the increasing DOC concentrations and coincident changes in stable isotope composition and vegetation seem to reflect a long-term increase of allochthonous organic matter loading and peat development in the watershed related to moister conditions during the past ca. 2000 years. As these results correspond to inferred moisture patterns in adjacent areas, fossil diatom assemblages in Levi Pond possibly recorded a larger regional moisture trend. More diatom-based long core studies in conjunction with stable isotopes and plant macrofossil analyses combined with a thorough investigation of climatic control on lake DOC are necessary to test the general usefulness of diatom-based DOC transfer functions as a paleohydrological proxy in temperate lakes. If hydrologically sensitive study sites are carefully chosen to avoid overriding eutrophication or acidification signals, fossil diatoms may be a promising additional proxy for future paleohydrological studies in temperate regions.

4.7.4 Regional versus local factors controlling New England lakes

Despite their proximity, the comparable elevation, lake morphology, watershed characteristics, and land-use history of Levi Pond and North Round Pond, their diatom communities displayed dissimilar trajectories during the past ca. 2000 years. These differences were caused by local differences in the extent and nature of human activities and interfering natural disturbances in the watershed, as well as differences in the time scale considered, whereas similarities derived from regional history.

In both lakes, diatom assemblages responded to logging in the watershed and partly recovered afterwards. This correspondence is expected due to the quite uniform land-use history across mountainous regions in New England. Another similarity was that algal communities did not completely return to pre-settlement conditions. This was probably due to natural disturbances and delayed recovery from acidification at North Round Pond and continued peat development at Levi Pond. Our results indicate that long-term trends in climate change and small-scale natural disturbance patterns did not only cause ecosystem variability in pre-settlement periods, but still contribute to dynamics of anthropogenic altered ecosystems and will likely continue to do so in the future. Also, such as noted by Francis and Foster (2001), disturbance events can change the trajectory of lake development, such as in North Pound Pond. These factors have therefore to be considered in management decisions for ecosystem conservation and restoration as being a part of the “natural state”.

Differences were observed in patterns of habitat availability, in the response to climate change and in the evidence for short-lived natural and anthropogenic disturbance. In Levi Pond, a long-term increase of planktonic taxa was associated with higher lake DOC, which in turn was coupled to increased moisture. The short-term increase of benthic taxa in North Round Pond, however, was probably related to increased macrophyte abundance and/or increased supply of allochthonous material from deforested areas. These differing patterns in habitat availability indicate that changes in life forms are controlled by diverse local factors and must therefore be interpreted with caution in the context of regional patterns or be combined with independent proxies, such as stable isotopes.

It is surprising that signs of lake acidification were seen only in North Round Pond and not in Levi Pond. However, Levi Pond may have acidified, too, but our model was not adequate for pH reconstructions because of poor analogs. It is possible that the massive deforestation caused by the 1938 hurricane enhanced acidification effects in North Round Pond, whereas the watershed of Levi Pond remained mostly forested during the period of acidic deposition.

A climatic signal was only recorded in Levi Pond in the form of a long-term moisture increase over the last ca. 2000 years. The fact that we did not find this pattern in North Round Pond may simply result from the shorter sedimentary record which did not provide comparison to the drier period before 0 AD. Also, the watershed morphology of Levi Pond is such that it may have favoured peatland development and therefore enhanced the moisture signal. Short-term climatic events, such as the Little Ice Age cooling, are not evident in our records, but the long-term moisture trend may be associated with the Neoglacial cooling recorded by paleoclimatic proxy records across north-eastern North America.

4.8 Conclusions

This study of fossil diatom assemblages in two small New England ponds has demonstrated complex limnological changes, which are related to a multitude of human and natural disturbances in the watershed as well as climatic change. The regional history of deforestation and subsequent reforestation was reflected in the diatom response and recovery in both ponds. Local factors, such as peatland development, macrophyte abundance and hurricane impact were likely responsible for differences in the diatom assemblage patterns between the lakes. A change to increased moisture was indicated by diatoms and pollen in Levi Pond, thereby recording a regional trend suggested by previous studies and underscoring the usefulness of these proxies for paleohydrological studies. Our study has also shown that diatoms provide independent evidence for natural disturbances and climatic change. Therefore, including them in paleoecological analyses of more lakes with equally long records will help generate a more comprehensive picture of factors controlling pre-settlement ecosystem variability in New England.

4.9 Acknowledgements

This research is part of a larger National Science Foundation, USA project (grant no. 9903792), which was initiated by Janice Fuller and David Foster and was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) through an operating grant to R. Pienitz. S. Clayden and J. McLaughlin counted the pollen of Levi Pond. We would like to thank S. Barry, E. Duthie and W. Oswald from Harvard Forest for lab and field assistance and for carrying out the LOI analyses and dating. N. Kamman from the Vermont State Water Department and M. S. Ford kindly provided water chemistry data for Levi Pond. We acknowledge logistic support provided by the Centre d'études nordiques, Québec, and Harvard Forest, Massachusetts. The quality of the manuscript was greatly improved by constructive critics from É. Saulnier-Talbot and S. Hausmann.

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5 Seasonal diatom variability and paleolimnological inferences - a case study

5.1 Résumé

Avec l’étude d’une séquence annuelle des diatomées et des diatomées fossiles de Bates Pond, Connecticut (États-Unis), les implications de la variabilité saisonnière des diatomées pour l’analyse paléolimnologique ont été évaluées. Les changements des assemblages diatomifères au cours d’une année étaient principalement liés à la stratification, mais aussi au nitrate, silice et phosphore. Les changements des assemblages fossiles ont reflété l’activité humaine dans le bassin versant et la récupération subséquente. L’interprétation à l’aide des préférences saisonnières des espèces suggère qu’une tendance à long terme reflète un changement du régime de brassage de l’eau pendant le Petit Âge Glaciaire. La majorité des diatomées a proliféré en automne ce qui indique que cette saison est préférable pour faire les analyses d’eau en vue du développement des fonctions de transfert. Cette étude préliminaire a montré que les informations sur la saisonnalité des diatomées peuvent fournir des renseignements pertinents pour les analyses paléolimnologiques.

5.2 Abstract

The seasonality of physical and chemical water parameters and aquatic organisms is a major characteristic of temperate, dimictic lakes, but only few investigations have considered the potential information that is encoded in seasonal dynamics with respect to the paleolimnological record. With the study of a one-year seasonal sequence of diatoms using sediment traps and the fossil diatom record covering the last 1500 years in Bates Pond, Connecticut, we investigated which factors control the seasonal distribution of diatoms and how this information can be used for the interpretation of the paleolimnological record. The

seasonal patterns in diatom assemblages were mainly related to changes in stratification and, to a lesser extent, to nitrate, silica, and phosphorus. During the full-circulation periods in spring and autumn, the richest diatom populations dominated by tychoplanktonic species developed and were only replaced by some lightly silicified, spindle-shaped planktonic diatoms during two months of thermal stratification in summer. Changes in fossil diatom assemblages likely reflected human activity in the watershed after European settlement and subsequent recovery in the last century. In addition, a long-term trend in diatom assemblage change initiated before European settlement was probably related to increased length of mixing periods during the Little Ice Age, such as indicated by the increase of taxa that presently grow during full circulation periods and by application of a preliminary seasonal temperature model. The study of limnological conditions and diatom succession in more similar lakes or over several years in one lake would be desirable in order to establish a more robust seasonal data set for the enhancement of paleolimnological interpretations. Also, the main part of diatom numbers has been deposited during autumn, whereas the spring assemblages were less numerous, but similar to autumn assemblages. This indicates that spring and autumn may be the best seasons for sampling of lakes with the purpose of developing diatom inference models in temperate, dimictic lakes. In conclusion, this study has shown that the investigation of seasonal diatom dynamics in temperate lakes may provide important information for the refinement of paleolimnological interpretations.

5.3 Introduction

In temperate regions, seasonality is a major characteristic of freshwater ecosystem dynamics (Wetzel 2001). The variability of the physical, chemical and biological conditions over the course of a year causes significant changes in the composition, biomass and number of dominant algal species (Sommer et al. 1986; Interlandi et al. 1999; Wetzel 2001). For example, different diatom species attain peak populations at different times during the annual cycle, thereby indicating different environmental conditions. As these patterns are integrated in surface sediment samples used for the development of diatom-based inference models and paleolimnological analyses, they introduce noise into the obtained signal (Hall and Smol 1999). The seasonally fluctuating parameters determine what is finally preserved in the sediments (Anderson 1995). Therefore, knowledge of the responses of the organisms to environmental variability at finer temporal scales is necessary for the interpretation of the paleolimnological record (Reynolds 1990). Although Smol (1990) stressed the need for more communication between ecologists and paleoecologists, few researchers have established this link between neo- and paleolimnological studies (Siver and Hamer 1992; Bradbury and Dieterich-Rurup 1993; Bennion and Smith 2000; Lotter and Bigler 2000; Pienitz and Vincent 2000; Bradshaw et al. 2002).

For the development of robust diatom-based inference models and for ecological interpretations of the fossil record, the knowledge of the autecological preferences of individual species is essential. As population responses at the seasonal scale are strongly controlled by species-specific physiological integration of smaller-scale, higher frequency stimuli (Reynolds 1990), the study of seasonal dynamics of algal communities and their relation to the environment may be useful for obtaining information on individual ecological preferences of species. To our knowledge, only few such studies of seasonal dynamics of algae with regard to their implications for paleolimnological analyses have been presented, such as for chrysophytes in a Connecticut lake (Siver and Hamer 1992) and for diatoms in a Swiss alpine lake (Lotter and Bigler 2000). Studies of parameters controlling the seasonal dynamics of phytoplankton, and particularly diatoms, were mostly conducted in large stratified lakes (Sommer 1986; Sommer et al. 1986; Kilham et al. 1996), whereas data about seasonal diatom succession in small, well-mixed North American lakes are rather sparse (Agbeti et al. 1997).

The need for high quality environmental data for the development of inference models has been emphasized by Birks (1998). Taking numerous water samples over the course of the year in order to obtain a representative average is one possibility to attain this objective (Bennion and Smith 2000). An alternative approach could be the consideration of the seasonality of algae. As diatoms in temperate lakes usually form dense populations only during certain seasons of the year (often in spring and autumn), the subfossil and fossil assemblages reflect most likely the limnological conditions of these seasons. For the development of diatom-based inference models, this means that the period when diatoms form the majority of their annual biomass would be most appropriate for sampling water for the measurement of physical and chemical variables. For existing inference models in temperate regions, there is no consensus with respect to the season when water chemistry samples should be taken. Sample timing differs from spring (Hall and Smol 1992; Lotter et al. 1998), summer (Dixit et al. 1999) and autumn (Kauppila et al. 2002) to mean annual values (Bennion 1994; Cameron et al. 1999). Bradshaw et al. (2002) presented a first comparison of different seasonal inference models for Danish lakes, but no such attempt has yet been made in North America.

The sediment trap technique is an effective method for studying seasonal dynamics of algae (Horn and Horn 1990). It can provide more detailed data at finer temporal scales for calibration of inference models (Smol 1990) and important information on taphonomic processes (Smol 1990; Ryves et al. 2003). With a one-year sediment trap study of diatom succession in Bates Pond combined with analysis of fossil diatoms preserved in the sediments of the same lake, we tried to answer the following questions: 1) Is it possible to identify ecological preferences of individual species for environmental variables based on a seasonal sampling strategy and use them in interpretations of the fossil record? 2) Which seasonal aspect of diatom assemblages is predominantly represented in the surface sediments and which season is thus most appropriate for water chemistry determinations for diatom-based inference models? 3) Do individual diatom species thrive in particular seasons and do they therefore indicate changes of the relative length of past seasons, if encountered in the fossil record?

5.4 Study site

Bates Pond (72° 6’ W, 41° 39’ N) is situated in southeastern Connecticut, USA, in the coastal plain of New England, at an elevation of 95 m a. s. l. (Fig. 5.1). The lake has a surface area of 2.7 ha and a maximum depth of ca. 3.6 m. Major lake and catchment characteristics are presented in Table 5.1. Dense macrophyte vegetation, composed mainly of *Nymphaea* and *Brasenia*, colonizes the littoral zone. The watershed is at present mostly covered by an deciduous forest dominated by oak, birch and pine, but includes also some lawn (Fig. 5.1 b).

Figure 18 Map of New England (USA) with the location of Bates Pond.

Table 5.1 Major lake and catchment characteristics of Bates Pond.
Values for water chemistry are annual means based on 11 measurements from March 2001 to April 2002 (Fig. 5.4). Values are given in mg l^{-1}, if not otherwise indicated. For a complete abbreviation list of limnological parameters see caption of Table 5.2.

surface area (ha)	2.7	SO_4^{2-}	7.9
Watershed area (ha)	68.2	SiO_2	2.7
Maximum depth (m)	3.6	Ca^{2+}	2.6
pH	6	Chl *a*	2.0
TP (μg l^{-1})	13.5	K^+	0.7
SRP (μg l^{-1})	3.7	Mg^{2+}	0.8
TN	0.4	Na^+	4.8
NO_2^--N (μg l^{-1})	3.3	DOC	5.9
NO_3^--N (μg l^{-1})	17.3	DIC	1.4
NH_4^+-N (μg l^{-1})	44.1	POC	0.5
Cl^-	7.2	Chl a (μg l^{-1})	2

Three houses and a gravel road, situated at the eastern end of the lake, do not contribute to the lake input, but drain into the outlet, which is situated at the southeastern end. Large parts of the watershed were cleared and used for agriculture by European settlers in the 18th and 19th century. In 1935, the Ginetti family acquired the lake and large parts of the watershed. At that time, the watershed was covered with young deciduous forest, which has matured until today.

5.5 Methods

5.5.1 Sampling and sample treatment

A sediment trap with three separate tubes was installed in Bates Pond on March 21st 2001, one day after ice-break-up. It was placed in the deepest part of the lake basin with the bottom of the trap at about 3 m depth, leaving about 2.5 m water column above the trap entry. We used a system with two anchors (Horn and Horn 1990), where one anchor holds the trap with a rope, and where the other end of this rope connects diagonally to the buoy located some meters beneath the trap, which in turn is kept in place by the second anchor (Fig. 5.2). This assembly precludes contamination by epiphytic algae growing on the rope when the buoy is installed directly above the trap. A conservation agent (Lugol's solution ®) was added to the bottom of each tube to prevent alteration of sedimented diatom assemblages by zooplankton grazing.

Sediment traps and lake water were sampled monthly during the ice-free season, except in January 2002, when the lake was frozen. The contents of the first and second tube were used for replicate diatom analyses. The material from the third tube and the sediment core samples were analyzed for sediment organic matter by loss-on-ignition at 550°C (Heiri et al. 2001). For diatom analyses, the trap samples were cleaned with 30% H_2O_2, and microscope slides were prepared after adding a known amount of microspheres (Battarbee and Kneen 1982).

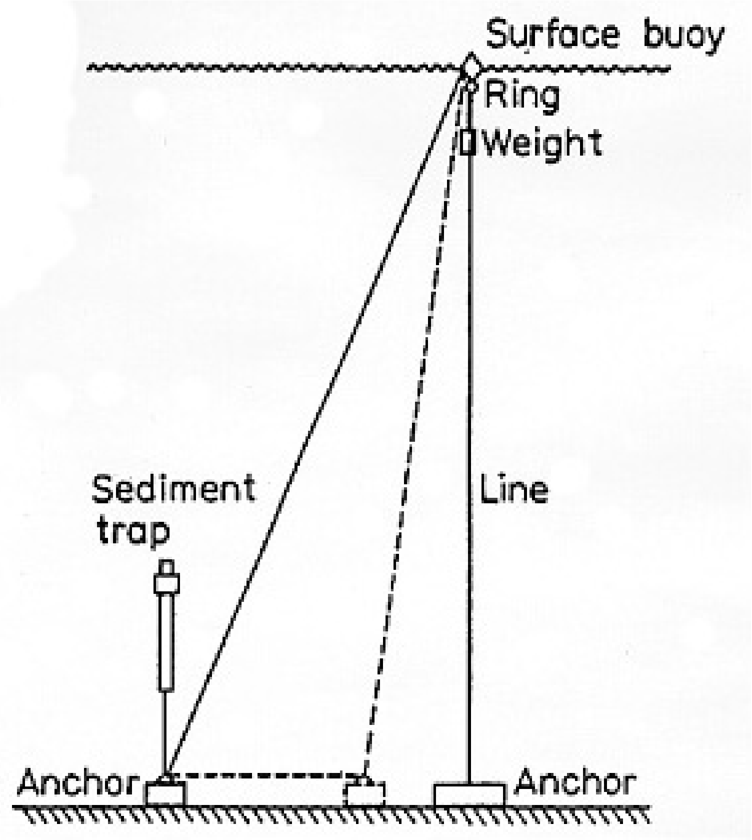

Figure 19 Deployment of the sediment trap.
Modified from Horn and Horn (1990).

A minimum of 300 valves was counted under oil immersion objectives using Leica DMRB in the Paleolimnology-Paleoecology Laboratory at Laval University. The mean counts of two replicate samples were used for calculating relative abundances and for numerical analyses. For absolute numbers, the mean daily accumulation rate per sampling period was calculated from the total diatom numbers in the sediment trap sample divided by the number of days of exposure, in order to take into account the different time lags between sampling intervals.

At each sampling date, vertical temperature, oxygen and conductivity profiles were taken at 50 cm intervals and surface water pH was measured using Quanta Hydrolab®. Water samples were taken from ca. 50 cm depth at the center of the lake, filtered the same day and sent to the National Laboratory of Environmental Testing, Burlington, Canada, for analyses of major ions, nutrients, dissolved organic and inorganic carbon (DOC, DIC), and chlorophyll *a* (chl *a*) according to standard procedures. In May 2000, a 1.65 m long sediment core was obtained from the deepest part of the lake basin using a clear Lexan coring tube fitted with a rubber piston. Sediment core slices were sub-sampled at 1 cm intervals and stored in plastic bags at 4°C. Diatom extraction followed standard strong acid digestion techniques (Pienitz et al. 1995), and a minimum of 500 valves per microscope slide were enumerated under 1000x magnification using the same material as used for the analyses of sediment trap samples. Species were identified according to standard and regional taxonomic references (Krammer and Lange-Bertalot 1986, 1988, 1991a, b; Camburn and Charles 2000; Fallu et al. 2000). The fossil assemblages were subdivided into diatom zones by optimal partitioning using the computer program ZONE (S. Juggins, unpublished program) and the number of significant zones was estimated by the broken-stick model (Bennett 1996).

5.5.2 Chronology

Bulk sediment samples were radiocarbon dated by accelerated mass spectroscopy at Beta Analytic Laboratories, Miami, Florida. Radiocarbon dates (^{14}C yr BP) were converted to calibrated years before present (cal. yr BP) using the computer program CALIB version 4.3 (Stuiver and Reimer 1993) and adjusted to calendar years (yr AD) by adding 50 years in order to permit consistent discussion of paleolimnological data in the historical context. The chronology of recent sediments was established by the ^{210}Pb technique and ages were calculated using a CRS point transformation model (Binford 1990). Settlement horizons were based on the rise of agriculture indicator pollen, such as *Ambrosia* and *Rumex,* and were assigned the date 1700 yr AD, based on foundation of the town of Canterbury. As the most recent ^{14}C dates based on bulk sediment show a large difference to the settlement date, probably due to an influence of old carbon) we discarded the date from 51 cm for our chronology and interpolated linearly between the minimum ^{14}C date in the 2 sigma range of the date from 77 cm, the settlement date and the oldest ^{210}Pb date.

5.5.3 Numerical analyses

The environmental data used for numerical analyses were mean values of the measurements of two consecutive sampling dates, i.e. the average of measurements at the corresponding sediment trap sampling date and the measurement taken one month before (two months before for February 2002). We have chosen this procedure in order to approximate as best as possible the conditions under which the diatoms had grown during the month before trap sampling. Conductivity, particulate organic matter (POC) and total dissolved nitrogen were excluded from the analyses, because data were missing for some sampling dates due to temporary technical problems with the conductivity meter and lost samples. The *in situ* measurements of dissolved oxygen and temperature at 0.5 m depth were used for numerical analyses in order to ensure comparability to water chemistry measurements, which were done at depth samples from the same depth. Dissolved oxygen concentrations were transformed to percent saturation using the temperature-dependent function of oxygen saturation of water (Wetzel 2001). An estimate for strength of stratification was calculated by subtracting the bottom water density from the surface water density, as calculated by the temperature-density function for freshwater at atmospheric pressure (Dokulil et al. 2001), and expressed by the density difference ($\Delta\rho$). The species data used for numerical analyses were mean percentages of two replicate counts, as described above.

Patterns in diatom assemblages and relationships of seasonal diatom communities to physical and chemical lake variables were explored using multivariate techniques implemented in the computer program CANOCO (ter Braak and Šmilauer 1998). The total amount of variation in seasonal diatom assemblages was assessed by detrended correspondence analysis (DCA) with detrending by segments. As the variation was relatively low with 1.67 standard deviations (SD), linear relationships of species to environmental gradients were presumed and therefore linear-based methods were applied in subsequent numerical analyses (Birks 1995). Relationships of seasonal diatom assemblages with environmental parameters were explored by redundancy analysis (RDA) in several steps. First, the combination of variables that are not colinear and which best explained the variation in diatom assemblages over the year was determined by stepwise backward selection. The variables that explained the least part of variation in the species data were subsequently removed until the variance inflation factors (VIF) of all included variables were less than 20. Dissolved oxygen was excluded from the selection because it is rather a response variable than a predictor in relation to algal communities. All subsequent analyses were carried out with the remaining four variables (stratification, total phosphorus, silica, nitrate) and temperature. Temperature was kept regardless of its high correlation with the variable "stratification", in order to demonstrate the effect of climatic variables on the assemblages.

Second, the amount of variance in the species data independently explained by each of these variables was estimated by RDAs with the first axis constrained to one variable (marginal effect) and by partial RDAs (pRDA), where the other variables were set to be co-variables (conditional effect). The significance of these relationships was tested using 199 Monte Carlo permutations adjusted for time series.

Third, the fossil diatom samples were included as passive samples in an RDA with the five variables mentioned above and the trap percentage diatom data, in order to assess the similarity of both sample sets. Sets of correlated environmental variables were identified using the environmental correlation matrix (Table 5.2).

Quantitative reconstructions of environmental variables and calculation of associated sample-specific reconstruction errors were carried out using the computer program C^2 (Juggins 2003). The pH and total phosphorus models using weighted averaging with inverse deshrinking and Gaussian logit regression, respectively, were based on a surface sediment diatom calibration set including 82 New England lakes (Köster et al. in press), which were selected a priori from a larger calibration set (Dixit et al. 1999) in order to limit its geographical extent to that of the paleolimnological study sites. Diatom-based inference models were developed for the variables that explained most of the variation in the seasonal data set using the linear method partial least squares regression (Birks 1995). These models were based on the same water chemistry and diatom data as used for ordination, as described above.

5.6 Results

5.6.1 Limnology of Bates Pond

Bates Pond was thermally stratified during sampling in April, July and August 2001, such as shown by the temperature isopleth diagram (Fig. 5.3) and the high density difference between epi- and hypolimnion (Fig. 5.4 a). During the other months of the year, there was no difference between surface and bottom water densities, indicating regular mixing of the entire water column.

The development of major water characteristics over the year is illustrated in Figs. 5.4 a-f. Oxygen saturation (data not shown) and inorganic matter content in the traps were high during the full-circulation periods in spring and autumn (May, October, November and February), when water column stability was low (Fig. 5.4 a). Inorganic matter in the sediment traps was observed at each sampling date, likely originating from suspended particulate inorganic matter and the inorganic parts of organisms, such as siliceous scales, cysts and frustules of chrysophytes and diatoms.

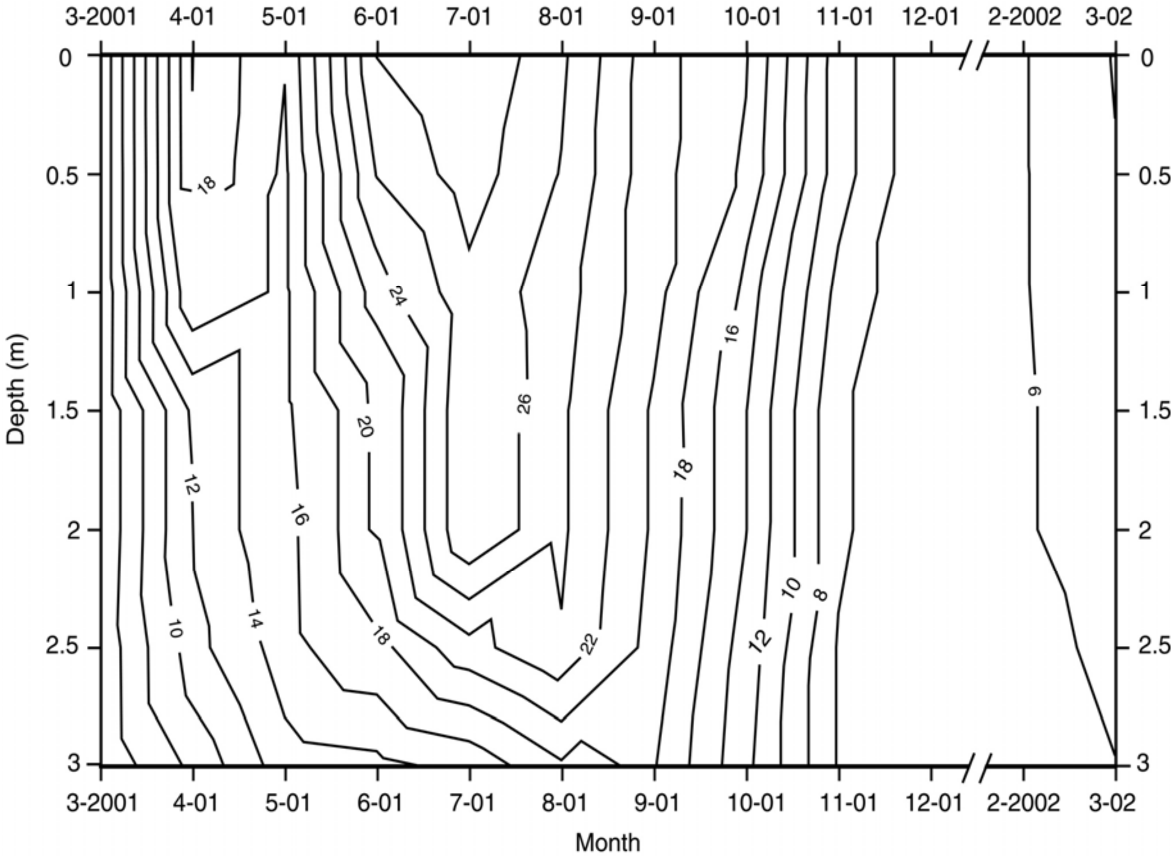

Figure 20 Temperature isopleths for Bates Pond from March 2001 to March 2002.
Note that data are missing for January 2002 due to the presence of ice cover. Temperature profiles were measured around noon at each sampling date.

Silicate (SiO_2) was highest in spring 2001, likely following increased run-off from the watershed (Fig. 5.4 b). It decreased until October, with a small peak in June, and increased from October 2001 to March 2002, possibly due to silica recycling during siliceous algal decay. Phosphorus was generally low with one peak of soluble reactive phosphorus (SRP; 20 $\mu g\ l^{-1}$) and total phosphorus (TP; 30 $\mu g\ l^{-1}$) in October (Fig. 5.4 c) during full fall circulation. Another peak of TP occurred in June (28 $\mu g\ l^{-1}$), when SRP was low, indicating that this TP increase was bound in particulate matter, such as algae or seston. High values in dissolved silica and POC at the same date (Fig. 5.4 b) indicate that there was a high sedimentary input from the watershed. Dissolved total nitrogen (TN) and nitrate (NO_3) were low during the spring and summer and increased during late autumn and winter (Fig. 5.4 d), probably reflecting enhanced decay of macrophytes and other biomass during autumn and winter. The major ions (here represented by Cl^-) and pH increased steadily from March 2001 to March 2002 (Fig. 5.4 e).

Aquatic primary productivity, as indicated by chlorophyll *a* (chl *a*; corrected for pheophytins), reached maxima in May, June and September (Fig. 5.4 f). Diatom productivity peaked from September through November, suggesting that the September maximum in chl *a* was formed by diatoms (Fig. 5.4 f). The diatom accumulation maximum in autumn correlates with a TP and SRP maximum in October. Chrysophyte scales and cysts were not quantified, but visibly dominated the cleaned sediment trap samples from May through October, indicating that blooms of these algae may have caused some of the observed Chl *a* maxima. However, high relative chrysophyte abundances were also found in months with low Chl *a* (July, August), indicating that other algal groups must also have contributed to the biomass peaks. As the inorganic matter content changed during the year (Fig. 5.4 a), it is possible that the relative abundance of algal groups with and without inorganic parts fluctuated.

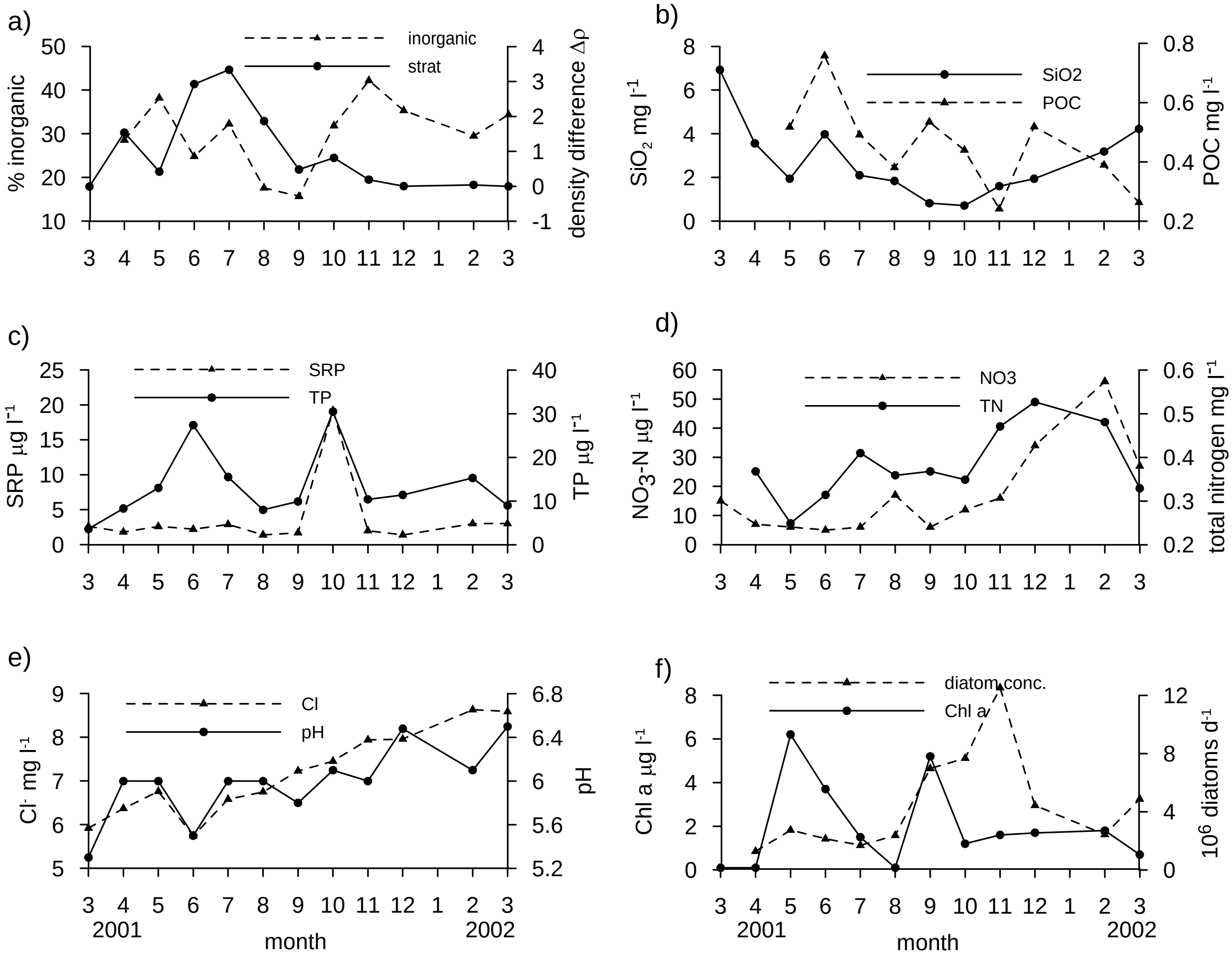

Figure 21 Seasonal variation of limnological parameters at Bates Pond from March 2001 to March 2002.

a) percentage of inorganic matter in the sediment trap (inorganic) and strength of stratification (strat) expressed as the difference between surface (0 m)and bottom (3 m) water density. b) silica (SiO_2) and particulate organic carbon (POC). c) soluble reactive phosphorus (SRP) and total phosphorus (TP). d) total dissolved nutrients and nitrate nitrogen (NO_3-N). e) chloride (Cl) and pH. f) chlorophyll *a* and monthly mean of daily diatom accumulation rate. Note that no measurement was taken in January 2002.

Numerous correlations between the measured variables are demonstrated in the environmental correlation matrix (Table 5.2). The major ions, nitrogen compounds and pH were highly correlated with the physical variables, such as temperature and stratification, whereas the inter-correlated variables DOC, DIC, phosphorus and SiO_2 were less correlated with the other variables.

Table 5.2 (next page) Correlation matrix of environmental variables measured monthly at Bates Pond from March 2001 to March 2002.
Cl = chloride, SO_4 = sulfate, SiO_2 = silica, Ca = calcium, Chl *a* = chlorophyll a, K = potassium, Mg = magnesium, Na = sodium, DOC = dissolved organic carbon, DIC = dissolved inorganic carbon, SRP = soluble reactive phosphorus, NO_2 = nitrite nitrogen, NO_3 = nitrate nitrogen, NH_4 = ammonia nitrogen, TP = total phosphorus, Temp = temperature, DO % = dissolved oxygen saturation, strat = stratification, expressed as density difference between epi- and hypolimnion. Significance levels are given by bold type ($p<0.05$) and * ($p < 0.001$).

	Cl	SO_4	SiO_2	Ca	Chl *a*	K	Mg	Na	DOC	DIC	SRP	NO_2	NO_3	NH_3	TP	Temp	DO %	pH	strat
Cl	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SO_4	**0.85***	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SiO_2	-0.28	0.15	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ca	**0.95***	**0.89***	-0.07	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chl *a*	-0.3	-0.26	-0.27	-0.32	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
K	**0.81**	**0.91***	0.09	**0.87***	-0.04	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Mg	**0.99***	**0.9***	-0.19	**0.97***	-0.31	**0.83**	1	-	-	-	-	-	-	-	-	-	-	-	-
Na	**1***	**0.88***	-0.24	**0.97***	-0.28	**0.85***	**0.99***	1	-	-	-	-	-	-	-	-	-	-	-
DOC	0.31	-0.17	**-0.68**	0.27	0.08	0.04	0.23	0.28	1	-	-	-	-	-	-	-	-	-	-
DIC	0.22	0.06	-0.59	-0.02	0.26	0.04	0.18	0.18	0.12	1	-	-	-	-	-	-	-	-	-
SRP	0.22	0.01	-0.52	0.05	0.06	-0.04	0.21	0.18	0.21	0.45	1	-	-	-	-	-	-	-	-
NO_2	0.55	0.27	-0.28	0.6	0.04	0.55	0.49	0.56	**0.78**	-0.08	-0.05	1	-	-	-	-	-	-	-
NO_3	**0.87***	**0.9***	0.12	**0.95***	-0.4	**0.87***	**0.9***	**0.89***	0.12	-0.03	-0.16	0.53	1	-	-	-	-	-	-
NH_3	0.48	0.5	0.06	0.42	-0.42	0.54	0.43	0.5	-0.02	0.23	-0.31	0.31	0.6	1	-	-	-	-	-
TP	-0.05	-0.25	-0.41	-0.07	0.53	0.02	-0.08	-0.05	0.53	0.17	0.6	0.44	-0.25	-0.38	1	-	-	-	-
Temp	**-0.74**	**-0.89***	-0.22	**-0.71**	0.35	**-0.82**	**-0.76**	**-0.76**	0.29	-0.24	-0.02	-0.17	**-0.79**	**-0.7**	0.3	1	-	-	-
DO %	-0.28	0.12	0.53	-0.2	0.11	0.17	-0.26	-0.22	**-0.69**	-0.38	-0.29	-0.34	-0.1	0.18	-0.2	-0.17	1	-	-
pH	**0.93***	**0.78***	-0.31	**0.9***	-0.28	**0.8**	**0.89***	**0.94***	0.33	0.08	0.03	0.58	**0.83***	0.59	-0.13	**-0.65**	-0.08	1	-
strat	**-0.75**	**-0.85***	0.04	**-0.65**	0.21	**-0.69**	**-0.77**	**-0.75**	0.3	-0.46	-0.22	0.03	**-0.65**	-0.49	0.31	**0.9***	-0.04	-0.62	1
	Cl	SO_4	SiO_2	Ca	Chl a	K	Mg	Na	DOC	DIC	SRP	NO_2	NO_3	NH_3	TP	Temp	DO %	pH	strat

5.6.2 Seasonal distribution of diatoms

The seasonal distribution of the dominant diatoms in terms of absolute and relative abundances in Bates Pond from April 2001 to March 2002 is illustrated in Figs. 5.5 a and b, respectively. During the spring and early summer, *Tabellaria flocculosa* var. *linearis*, *Eunotia pectinalis* var. *undulata*, and *Eunotia* spp. (see Table 5.4 for authors) dominated the assemblages in relative and absolute numbers. A peak of *Asterionella ralfsii* var. *americana* followed in July and August and a maximum of *Nitzschia gracilis* appeared in September. During autumn, the relative abundances of *Cyclotella stelligera*, *Aulacoseira* spp. and *Fragilaria* spp. increased. Winter assemblages were dominated by *Cyclotella stelligera*, *Aulacoseira* spp. and *Eunotia* spp. in relative abundances. The absolute numbers of all species were highest from October to December. Total abundances decreased during winter, but *Cyclotella stelligera* and *Aulacoseira* spp. were more abundant in winter than in spring and summer.

5.6.3 Diatom-environment relationships

The environmental variables that are not colinear and explain most of the variance in the seasonal distribution of diatom assemblages from Bates Pond were stratification, nitrate, silica, and total phosphorus, as indicated by backward selection in subsequent RDAs. Of these variables, stratification accounted independently for the highest proportion of variance in the species data (15 %), followed by nitrate (12.4 %), silica (7.8 %) and total phosphorus (4.8 %), as indicated by partial RDAs (Table 5.3). While temperature was strongly correlated with stratification, it still explained 5 % of the species variance after partialling out the effect of the other variables. These results are illustrated in the environment-sample biplot (Fig. 5.6), where stratification and temperature were strongly correlated with species axis 1 ($r = 0.90$ and 0.76, respectively), NO_3 with species axis 2 ($r = - 0.63$), silica with species axis 3 ($r = -0.53$) and total phosphorus with axis 4 ($r = 0.42$). The eigenvalues of the first (0.53) and the second RDA axes (0.14) were very different indicating that the variables associated with the first axis explained the major part in the diatom assemblages compared to variables associated with further axes. However, these results have to be viewed with caution, because correlations between stratification and the other variables were detected (Table 5.2).

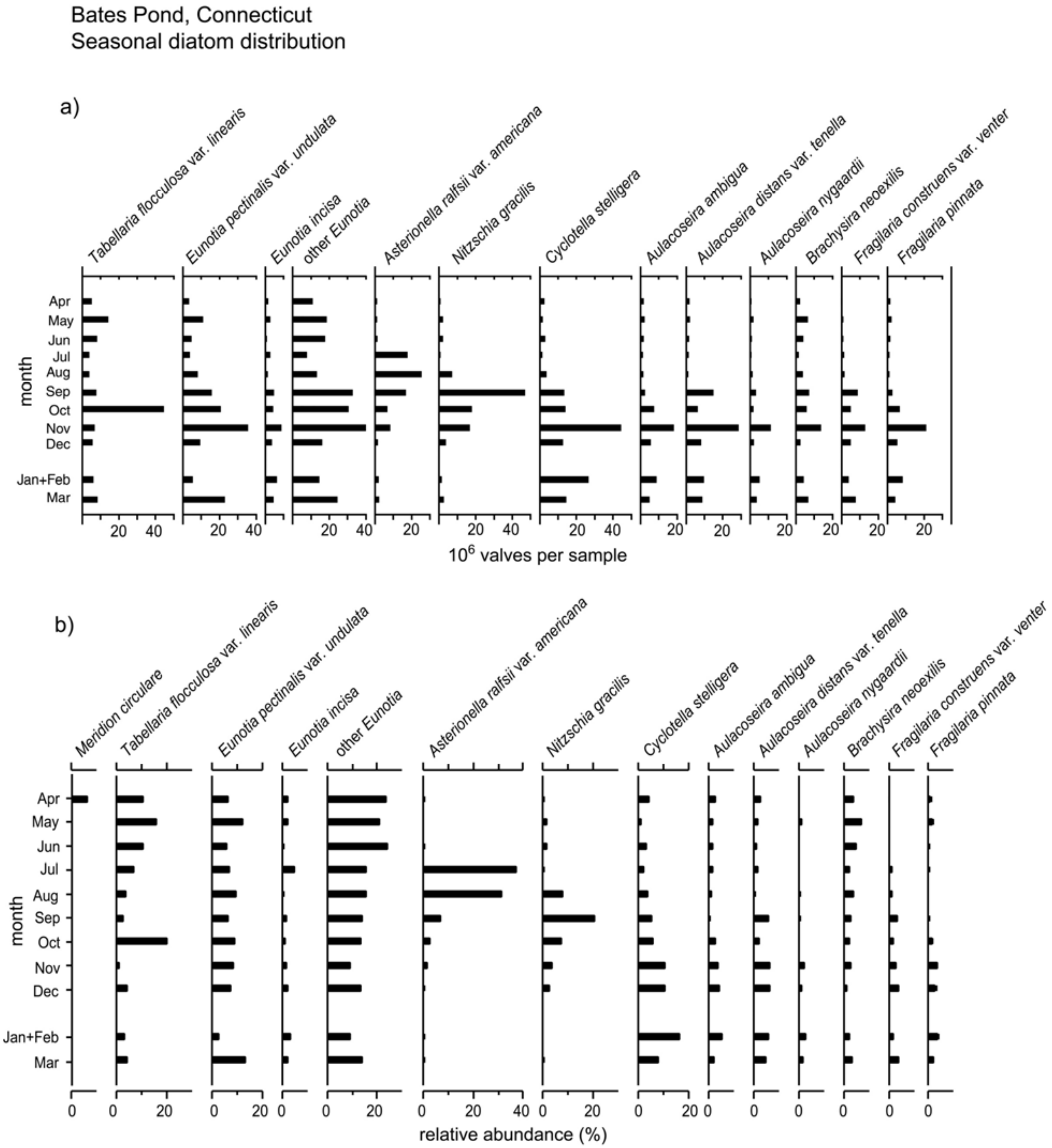

Figure 22 Seasonal distribution of the most abundant diatom taxa collected monthly in sediment traps. a) total abundance. b) relative abundance (% of the total number of valves). The absolute abundance is the mean daily accumulation per sampling period (see methods for details).

The only variables that explained significant portions of the species variance as assessed by Monte Carlo permutations were stratification and temperature (Table 5.3), with the highest influence shown by stratification. This suggests that stratification independently explained most of the variation and that the importance of the other variables (temperature, TP, NO_3) was partly due to correlation with stratification (Table 5.2).

The individual relation of the most abundant diatom species to the environmental variables is illustrated in the species-environment biplot (Fig. 5.7) and in Table 5.4. Many species were negatively correlated with stratification and temperature, because they flourished in autumn and winter, such as *Aulacoseira distans* var. *tenella, A. ambigua, Fragilaria pinnata*, and *Cyclotella stelligera*. *Asterionella ralfsii* was positively correlated with stratification and temperature, reflecting its appearance in summer. Species that were additionally related to NO_3 are *Cyclotella stelligera*, *Fragilaria pinnata* var. *lancettula* (positively) and *Tabellaria flocculosa* var. *linearis* (negatively) (Table 5.4).

Table 5.3 Results of ordination using redundancy analyses and Monte-Carlo permutation tests for assessing significance of environment-species relationships.
% explained: percentage of variance in species data that is explained by this variable, in pRDA after partialling out the effect of the four covariables.

variable	RDA one variable		pRDA (4 covariables)	
	% explained	p-value	% explained	p-value
stratification	48.6	0.085	15.6	0.04
temperature	38	0.04	5.2	0.075
NO_3	16.8	0.36	12.4	0.33
SiO_2	7	1	7.8	0.21
TP	4.9	0.83	4.8	0.51

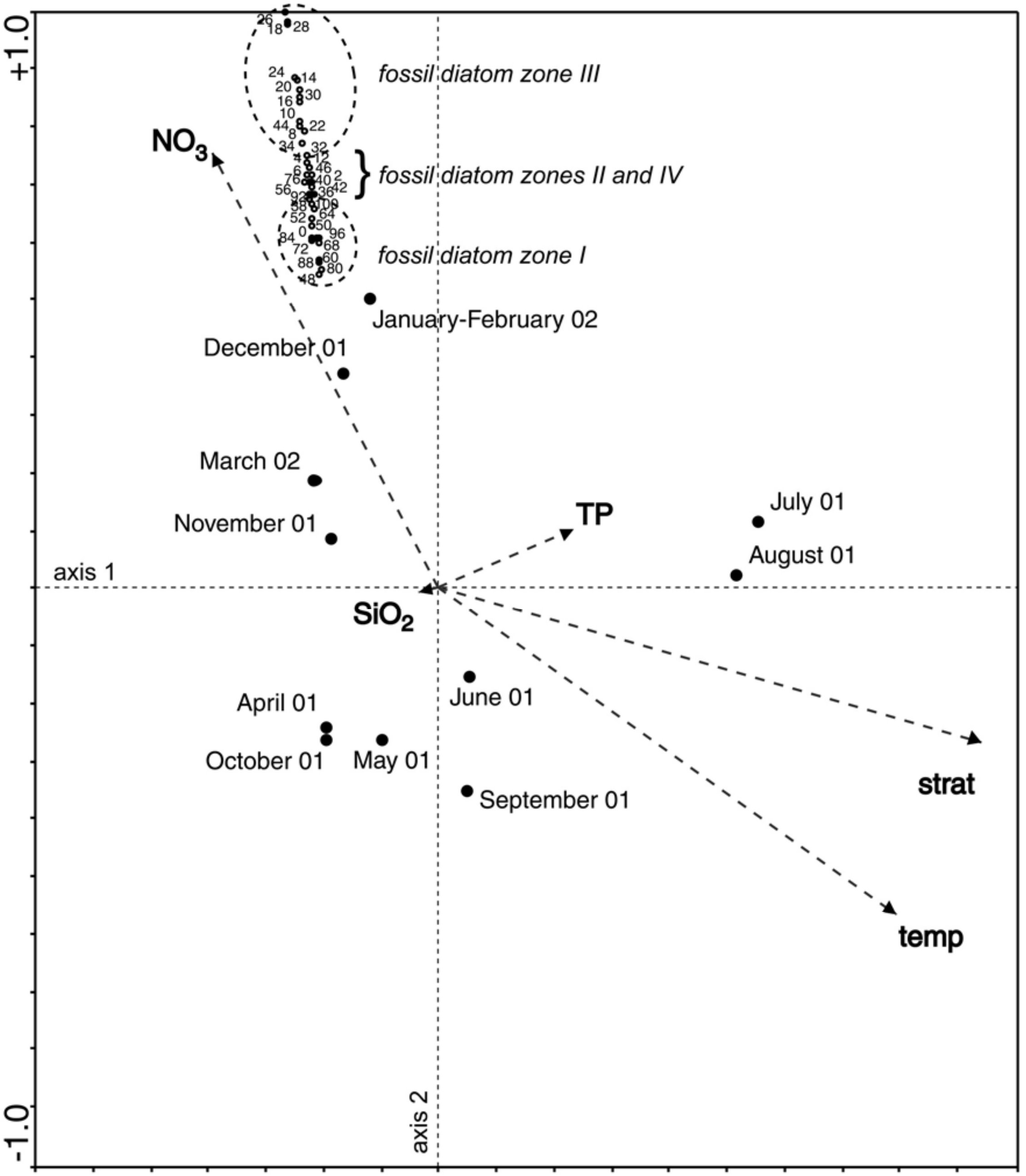

Figure 23 Environment-sample biplot derived from RDA of relative diatom abundances in the trap, fossil diatom samples and monthly environmental variables, with trap-diatom samples set as active samples and fossil diatom samples as passive samples.

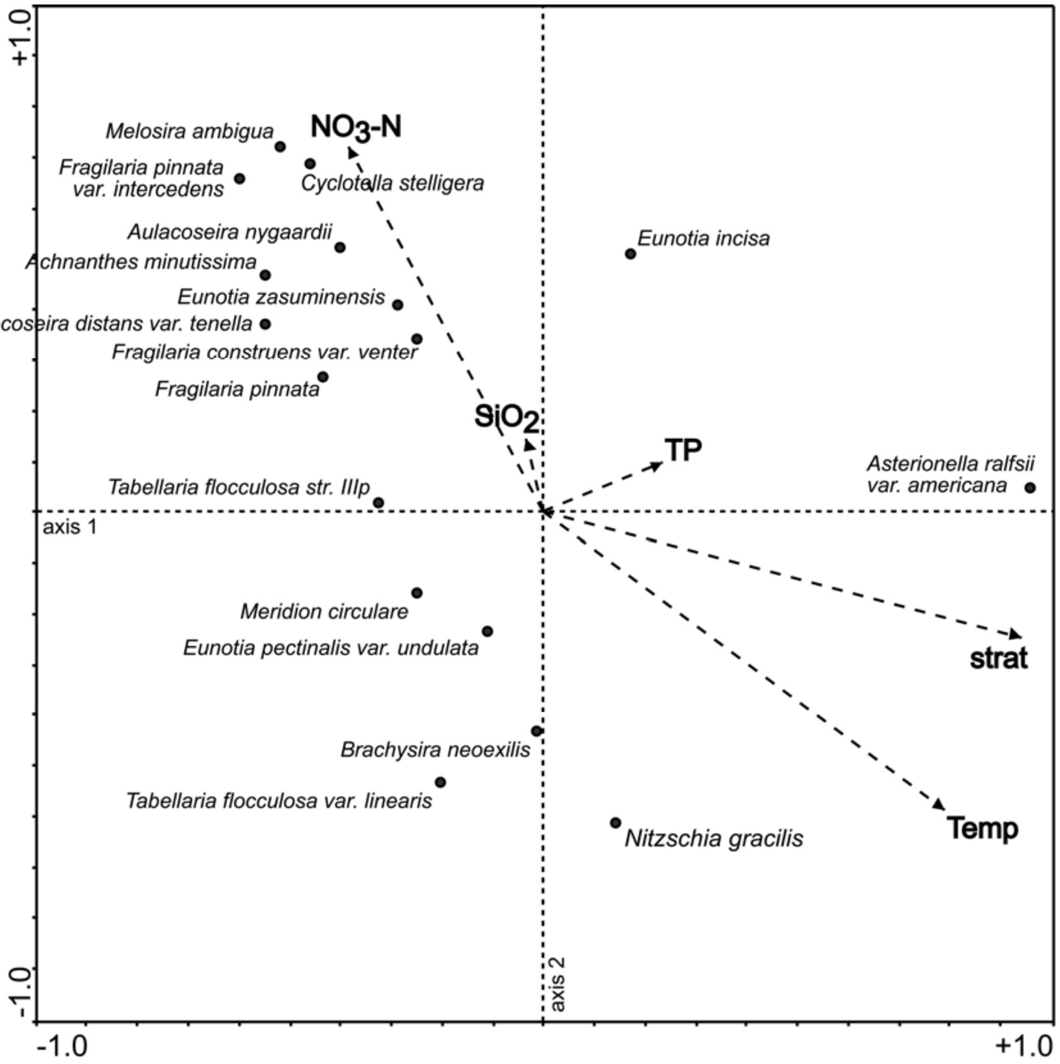

Figure 24 Environment-species biplot derived from RDA of relative diatom abundances in the trap and monthly environmental variables.

Species that are plotted close to the arrow head of an environmental variable are positively correlated with this variable, whereas species plotted at the opposite side of the axes' origin are negatively correlated with the same variable.

Table 5.4 Correlation coefficients between the most abundant species in the sediment traps and five environmental variables.

The values are derived from an redundancy analysis with centering and standardization by species. strat = stratification. temp = temperature. Significance levels are given by bold type ($p<0.05$) and * ($p < 0.001$).

taxon	strat	temp	NO_3^-	SiO_2	TP
Asterionella ralfsii var. *americana* Körner	**0.89***	**0.73**	-0.34	-0.03	0.24
Aulacoseira ambigua (Grun.) Simonsen	**-0.64**	**-0.78**	0.59	-0.08	0.11
Aulacoseira distans var. *tenella* (Nygaard) Florin	**-0.7**	**-0.65**	0.58	-0.3	-0.18
Aulacoseira nygaardii Camburn *in* Camburn and Kingston	-0.6	-0.63	**0.7**	-0.19	-0.1
Brachysira neoexilis Lange-Bertalot	0.16	0.2	-0.36	0.38	-0.2
Cyclotella stelligera (Cleve and Grunow) Van Heurck	**-0.69**	**-0.76**	**0.81**	-0.23	-0.02
Eunotia flexuosa (Brébisson) Kützing	-0.01	0.05	-0.39	0.27	0.09
Eunotia incisa Gregory	0.07	-0.18	0.26	0.29	0.04
Eunotia pectinalis var. *undulata* (Ralfs) Rabenhorst	-0.07	0.03	-0.05	0	-0.1
Fragilaria construens var. *venter* (Ehrenberg) Grunow	-0.45	-0.39	0.56	-0.43	-0.03
Fragilaria pinnata Ehrenberg	-0.39	-0.44	0.06	-0.02	0.12
Fragilaria pinnata var. *lancettula* (Schumann) Hustedt	**-0.76**	**-0.81**	**0.69**	-0.25	0.1
Nitzschia gracile Hantzsch	0.13	0.45	-0.26	-0.56	-0.2
Tabellaria flocculosa (Roth) Kützing str. IIIp sensu Koppen	-0.28	-0.31	0.23	0.44	-0.17
Tabellaria flocculosa var. *linearis* Koppen	0.03	0.2	-0.46	0.05	0.15

5.6.4 Lithology and chronology

The radiocarbon dates, calibrated and assigned dates are given in Table 5.5. The ^{14}C date of the 51 cm sample was older than the pollen-established settlement horizon. As the *Poaceae* profile showed the same settlement pattern as many other New England sites, we presumed that the ^{14}C date of the 51 cm sample is probably too old and we therefore omitted it in the chronology. Given the possibility that this was due to an influence of old carbon, we drew the linear interpolation line through the youngest date of the 2-sigma error range of the 77 cm sample. The complete chronology of the sediment core established by ^{14}C, ^{210}Pb and the settlement dates is illustrated in Fig. 5.8.

Organic matter content was relatively stable with about 40% from 100 to 60 cm depth (Fig. 5.9). It shows a small increase around 55 cm (shortly after settlement) and a gradual increase from ca. 40% at 45 cm (ca. 1750 AD) to ca. 50% at 18 cm (ca. 1885 AD), including a small peak of ca. 48% at 32 cm (ca. 1810 AD). Starting from 18 cm on, LOI decreased until it reached pre-settlement values (40%) from 11 cm depth (ca. 1930 AD) to the surface.

Table 5.5 Radiocarbon (^{14}C) dates for the Bates Pond core.

depth (cm)	Dated material	^{14}C yr BP	2 sigma range cal. Yr BP	Assigned age cal. yr BP	yr before 2000	yr AD
51	Organic sediment	442 ± 34	463-532	510	560	1440
77	Organic sediment	957 ± 73	744-952	740	790	1210
211	Plant macrofossil	1930 ± 40	1960-1810	1880	1930	70

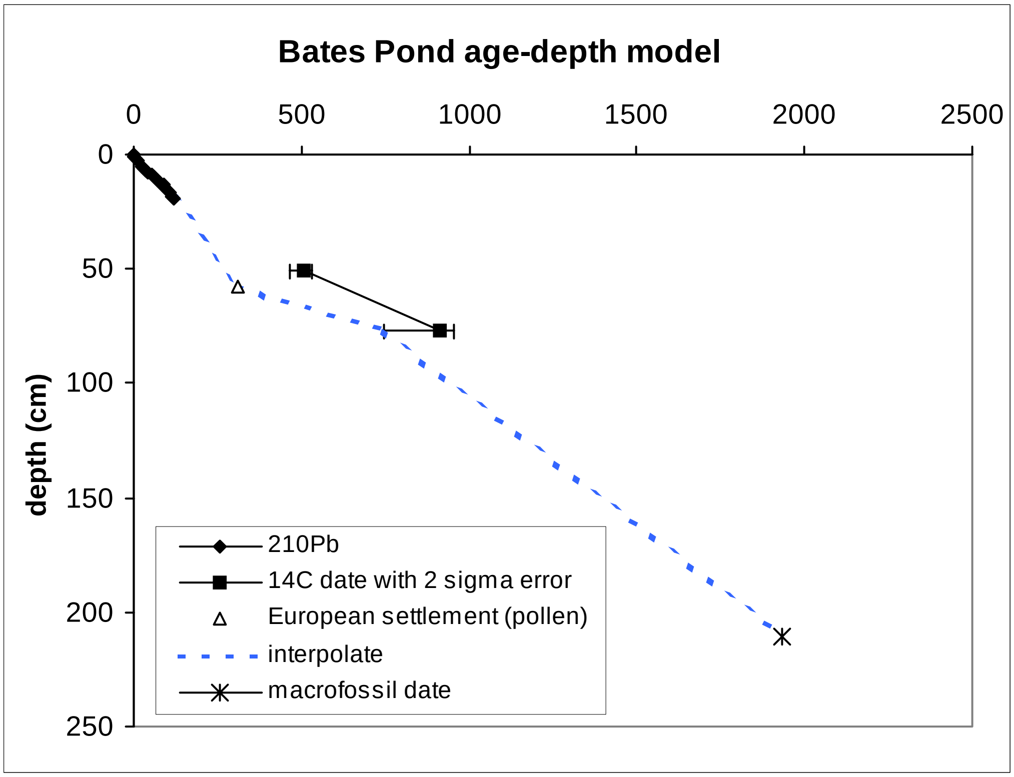

Figure 25 Chronology for the Bates Pond core based on Radiocarbon (^{14}C) and ^{210}Pb dates as well as pollen based settlement date.
See Fig. A.4 in the appendix for detailed ^{210}Pb results.

5.6.5 Fossil diatom assemblages

Fossil diatom samples of Bates Pond have been subdivided into four zones with significant changes in assemblages (Fig. 5.9). In Zone I (100 - 64 cm, ca. 1050 - 1550 AD) the diatom assemblages were dominated by *Cyclotella stelligera*, *Aulacoseira distans* var. *tenella*, and *Fragilaria pinnata. Tabellaria* spp., *Brachysira* spp. and *Eunotia* spp. were present in low abundances. In zone II (64 - 36 cm, ca. 1550 - 1800 AD), *Fragilaria pinnata* and, to a lower extent, *Eunotia zasuminensis* (Cab.) Körner increased at the expense of *Aulacoseira distans* var. *tenella.* Zone III (36 - 12 cm, 1800 - 1930 AD) is characterized by temporary increases of *Cyclotella stelligera, Aulacoseira ambigua*, and *Eunotia zasuminensis.* The assemblage composition of the fourth zone (12 - 0 cm, 1930 - 2000 AD) returns approximately to relative abundances observed during zone I (Fig. 5.9), with decreases of *Cyclotella stelligera, Eunotia zasuminensis, Aulacoseira ambigua,* and *Fragilaria pinnata,* and increases of *Eunotia incisa* and *Aulacoseira distans* var. *tenella*.

Diatom-inferred total phosphorus fluctuated between 15 and 20 µg l^{-1} (Fig. 5.9), indicating that the lake has been mesotrophic throughout the last ca. 1500 years. Diatom-inferred pH was equally constant with values between 7.2 and 7.5, but showed a slight increasing trend from the bottom to the surface of the core.

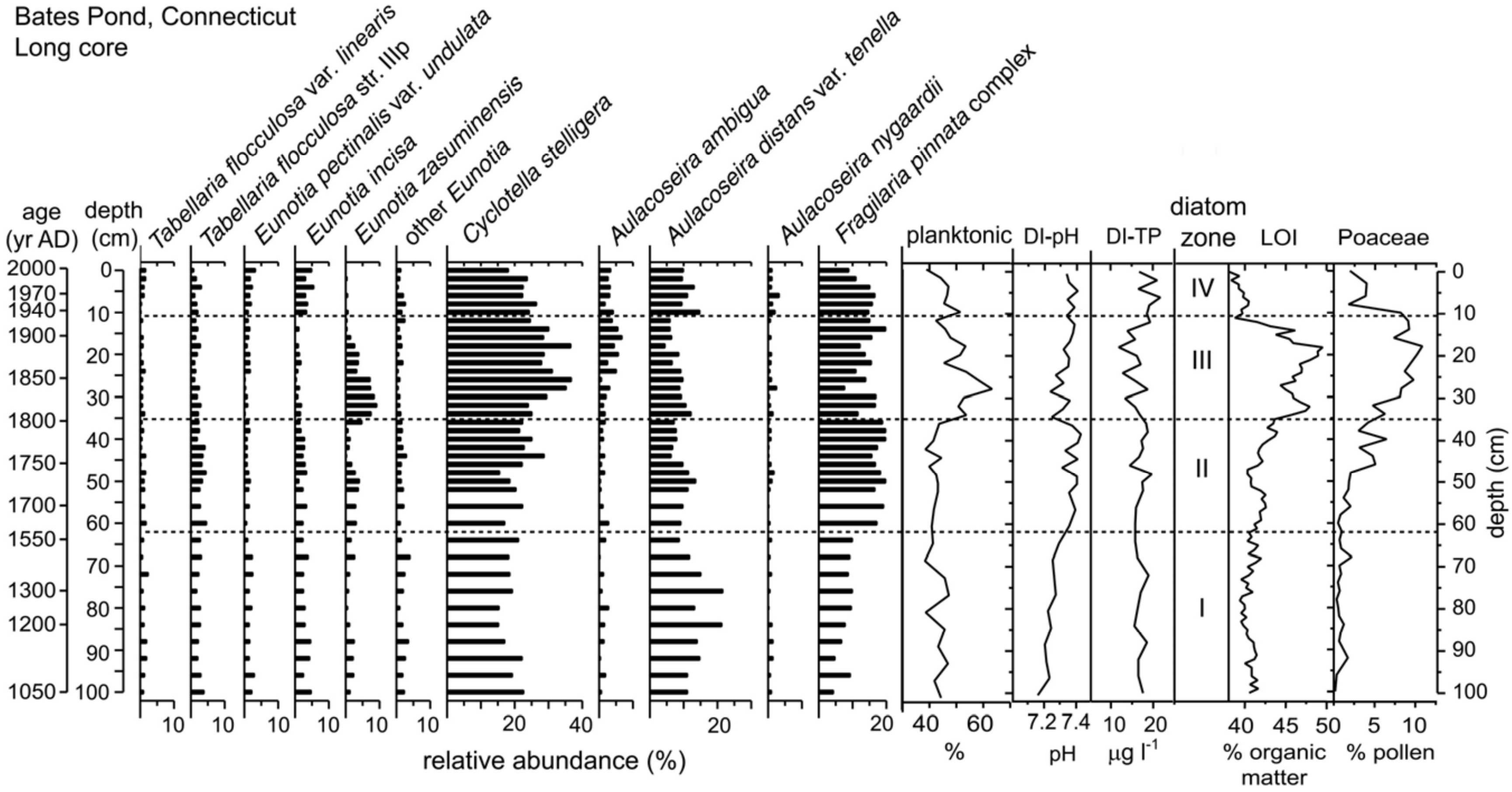

Figure 26 Fossil diatom assemblages from the sediment core of Bates Pond, percentage of planktonic species, diatom-inferred pH and TP, major diatom zones, and organic matter content estimated by loss-on-ignition (LOI).

5.6.6 Comparison of trap and sediment samples

In general, most species that are present in the sediment record were also found in the sediment traps, indicating that the lake core provided an accurate guide to the diatom species in the water column. However, in an RDA with trap samples used as active and fossil samples used as passive samples, the squared residual distances of the fossil samples to axes 1 - 4 were higher than the maximum distance of the modern samples to the axes, indicating very poor analogs (Birks et al. 1990). The reason for this is that several species were present in different relative abundances in core and trap samples. For example, the species dominating the sediment traps during warm periods in spring (*Tabellaria* spp.*)* and during summer (*Asterionella ralfsii, Nitzschia gracilis)* were rare in the sediments. (Figs. 5.5 and 5.9). In return, *Cyclotella stelligera* and epipelic diatoms, such as *Navicula* spp., were more abundant in the sediments than in the traps.

In ordination, the core samples are situated at the edge of the modern environment-sample space, close to the modern autumn and winter samples, indicating that the fossil samples are dominated by diatoms that presently grow during autumn and winter. There is a trend of fossil samples from 72 to 100 cm (diatom zone I) to align in such a way that places them more closely to the axis origin (corresponding to conditions of stronger stratification, lower NO_3) and the samples from 10 to 30 cm (diatom zone III) at the outside of the ordination space (corresponding to weaker stratification, higher NO_3).

The best performance of the PLS models based on trap diatom data and water chemistry was displayed by those with stratification, temperature, and NO_3 (Table 5.6), whereas the performance of the TP and SiO_2 models was lower (data not shown). Cross-validation was not possible because of an insufficient number of samples in the model, and therefore only apparent performance statistics are presented. As stratification is not a standard variable, we present only the reconstructions for temperature which, because of its high correlation to stratification, can therefore be used as a surrogate for the water column stability. As would be expected from their correlation, the reconstructions of temperature and NO_3 using the respective PLS models resulted in highly correlated inferences (Fig. 5.10). However, while inferred temperature showed a gradual decreasing trend from 100 to 20 cm depth and then an increase towards the top, nitrate remained stable from 100 to 50 cm and increased later than temperature, from 50 to 28 cm, and then decreased from 28 to 0 cm. The inferred temperature and NO_3 changes remained within the root mean square error of the model.

Table 5.6 Performance of the partial least squares models based on monthly diatom samples from April 2001 to March 2002 and associated water parameter measurements.

variable	model	RMSE	r^2	Ave Bias	Max Bias
stratification	PLS Component 1	0.23	0.95	0.00	0.62
	PLS Component 2	0.08	0.99	0.00	0.12
temperature	PLS Component 1	2.61	0.88	0.00	4.16
	PLS Component 2	0.68	0.99	0.00	0.48
NO_3	PLS Component 1	6.82	0.74	0.01	11.07
	PLS Component 2	3.55	0.93	0.00	7.09

RMSE = apparent root mean square error. r^2 = apparent coefficient of determination of the regression of predicted on observed values. Ave Bias = mean bias. Max Bias = maximum bias.

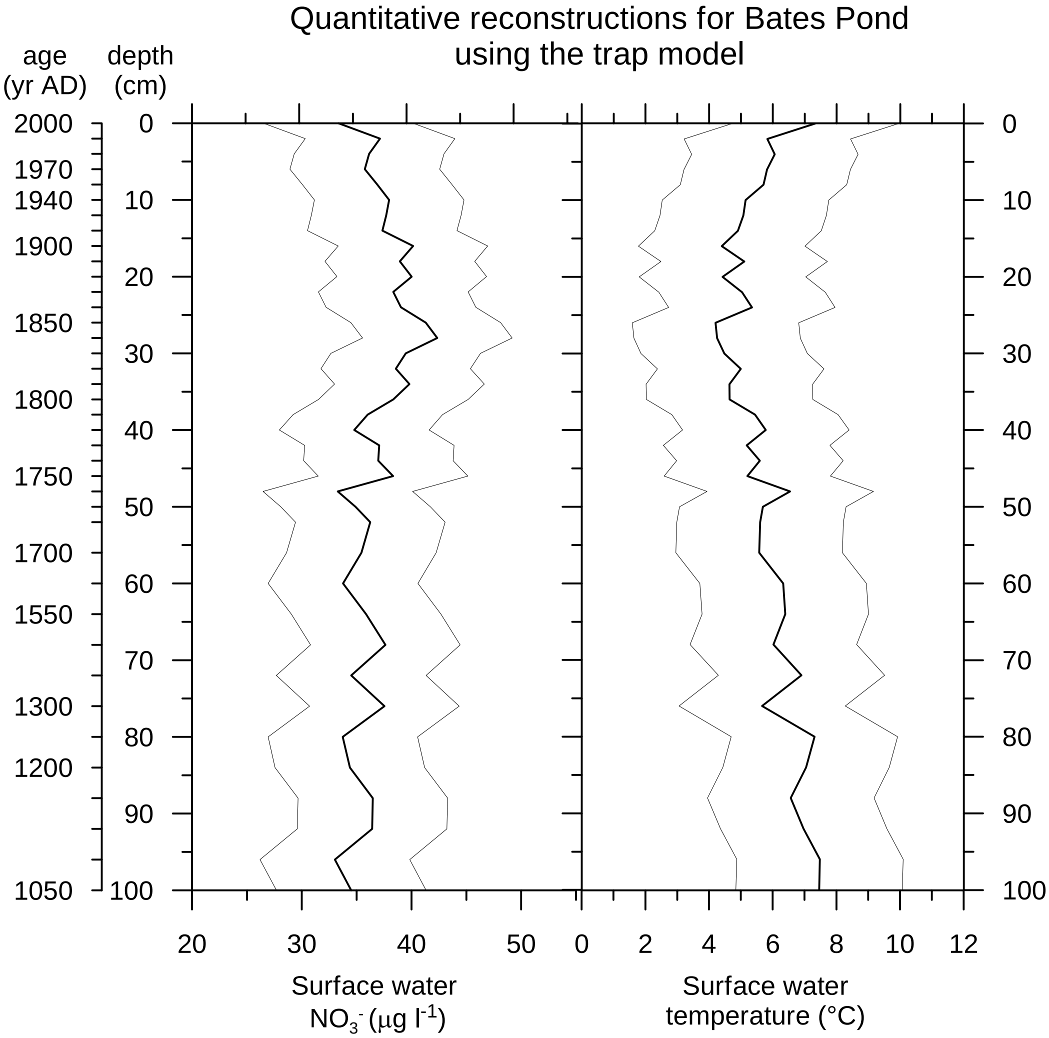

Figure 27 Quantitative reconstructions for surface water nitrate (NO_3^-) and temperature for the fossil samples of Bates Pond, using a PLS model based on 11 sediment trap samples and monthly water analyses.

Fine lines indicate the estimated root mean square error ranges of the models (see Table 5.6).

5.7 Discussion

5.7.1 Patterns and causes of seasonal diatom distribution

The seasonal distribution of most diatom species is related mainly to changes in both the physical environment (temperature, stratification) and NO_3 (Fig. 5.7, Table 5.4), which in turn is related to the major ion concentrations and pH (Table 5.2). The strong control of physical factors on diatoms is expected for a relatively shallow lake like Bates Pond, because shallow lakes can have full circulation throughout the entire year and most algae, in particular diatoms, rely on water turbulence for maintenance in the water column (Scheffer 1998). During periods of high water turbulence, such as during October and November, but also in short-term storm events in spring or summer, previously deposited tychoplanktonic diatoms are resuspended into the water column and can multiply to form rich populations (Smetaček 1985; Carrick et al. 1993). Periods with high water column stability were probably not long enough to cause nutrient limitation and hence nutrient competition between species (Scheffer 1998). Absolute diatom numbers were strongly correlated with a phosphorus peak in October as assessed by a RDA using absolute diatom abundances (data not shown), but this was true for all species and therefore phosphorus did not significantly influence the relative species composition (Table 4.3). Algae-environment relationships in a seasonal study of two oligotrophic Ontario lakes were similar to those observed in Bates Pond, with a high influence of temperature in the shallow and frequently mixed lake in contrast to stronger nutrient influence in a deep, stratified lake (Agbeti et al. 1997). Also, the presence of lightly silicified, spindle-shaped diatoms, such as *Asterionella ralfsii* and *Nitzschia gracilis* during summer in Bates Pond, were related to stratification in that study (Agbeti et al. 1997). Therefore, water column stability related to temperature and probably wind patterns seemed to be a major factor in determining changes in diatom assemblage composition in Bates Pond.

The presence of benthic species, such as *Brachysira* spp. and *Eunotia* spp., in the traps throughout the year and clearly higher total abundance of diatoms in the traps during autumn suggests that horizontal transport of benthic diatoms has occurred and that resuspension has probably influenced the observed seasonal dynamics. Dead cells in relation to living cells would have to be counted and identified in order to estimate the exact portion of trapped diatoms that were resuspended, non-living material and can thus not be related to the measured environmental variables. Analyses of the upper 1 cm of sediments in Hagelseewli, Switzerland, showed that the majority of small *Fragilaria* spp. were alive, whereas *Cyclotella comensis* populations consisted of about 50% living and 50% dead cells in depths from 0 to 10 m (Christian Bigler, personal communication), indicating that surface sediment assemblages can survive at the sediment surface until the next mixing event. Such analyses of fresh material were not carried out in our study. However, as resuspension results mainly from mixing patterns during colder months and allows growth of diatoms that would otherwise be lost by sedimentation, the influence of resuspension on the observed seasonal patterns can be regarded as evidence for the physical (climatic) factors controlling diatom assemblages in Bates Pond.

For comparison with the long-term record of Bates Pond it would be of advantage to know the one-year pattern observed here is also representative for other years. In the absence of major human or climatic disturbances, seasonal patterns in lake phytoplankton are similar from one year to another (Wetzel 2001). A study of varved sediments in a deep Finnish lake showed similar patterns in diatom assemblages over several consecutive years (Simola 1979). Also the algae in a shallow, frequently mixed lake show similar patterns from year to year (Agbeti et al. 1997). However, shallow lakes are more susceptible to stochastic events such as strong winds, and therefore may have less long-term stability in species composition and annual cycles than deeper lakes, particularly if turbidity increases due to resuspended sediments in the water column (Sommer et al. 1986; Carrick et al. 1993; Scheffer 1998). At Bates Pond, the large Secchi depth values on several occasions (March = 2.7 m; April = 3.5 m; June = 2 m; December = 2.7 m) indicate adequate light for photosynthesis even at the bottom of the pond. Still, the study of at least one supplementary year would be desirable for testing the hypotheses developed here regarding the controlling environmental factors for diatom assemblages in Bates Pond.

5.7.2 Fossil diatom assemblages

From 100 cm (ca. 1050 AD) to the present, diatoms indicate relatively stable oligotrophic to mesotrophic conditions and a circumneutral pH. However, diatom assemblages responded to human disturbance in the watershed, as discussed below. PCA scores show an additional gradual trend from 80 cm on (data not shown), which continues through zone III and II.

The diatom assemblage change at 60 cm (ca. 1700 AD) and a temporal increase in sedimentary organic matter content (Fig. 5.8) occurred coincident with increases of *Secale*, *Ambrosia*, and other Poaceae pollen (Fig. 5.8) and are therefore likely related to European settlement. *Eunotia zasuminensis* increased also significantly in response to human activity in the watershed in zone III. *F. pinnata* has been observed as a result of Hemlock (*Tsuga*) decline in Ontario lakes and coincident with logging and increased charcoal abundance at North Round Pond, New Hampshire (Köster, chapter 4). The charcoal:pollen ratio in Bates Pond did not change during this period; therefore deforestation is the most likely cause for this species change.

The most evident change in Bates Pond diatom assemblages with increased abundances of *Cyclotella stelligera, Aulacoseira ambigua,* and *Eunotia zasuminensis* coincided with increased agricultural activities in the watershed. *Cyclotella stelligera* has increased following logging in Walden Pond, Massachusetts (Köster, chapter 3). *Aulacoseira ambigua* is a tychoplanktonic species, which can thrive in oligo- to mesotrophic waters. It may therefore have been favored by a slight increase in nutrient availability due to increased inputs of allochthonous matter from deforested and cultivated land. *E. zasuminensis* has a preference for slightly dystrophic waters (Nicholls and Carney 1979; Eloranta 1986) and may therefore indicate increased dissolved organic carbon (DOC) concentrations, as deforestation in the catchment of lakes may lead to increased inputs of soil decomposition products (Carignan et al. 2000). Diatom-based quantitative inferences of DOC in Levi Pond, Vermont, indicate increased DOC following logging in the watershed (Köster, chapter 4). No reliable inference can be made about DOC responses to catchment modification in this pond, because of poor analogs of the fossil samples to the DOC model used in this study (Köster, unpublished data).

As all of the species that increased in zone III are planktonic, they may also have responded to a higher availability of pelagic habitat or higher water turbulence. The opening of the landscape can increase the exposure of the lake to strong winds, which may have caused stronger circulation in the water column and thus enhanced proliferation of planktonic algae.

Also, lower water temperatures could have prolonged full circulation periods, such as discussed below.

The return of diatoms to early settlement assemblages during the 20th century indicates an almost complete recovery of the lake following reforestation of the watershed. The current residential use of the lake is limited to the members of one family with only a few buildings that are not situated in the watershed of the lake. It appears that the low impact of the proprietors has largely contributed to the dilute character of the lake, an exemption amongst Connecticut surface waters which are usually moderately to heavily affected by eutrophication (Siver et al. 1996; Trench 1996).

5.7.3 Implications of seasonal diatom patterns for paleolimnological inferences

The seasonal patterns in the diatom assemblages were mainly controlled by changes in the physical environment, such as stratification, which in turn affected the development of water chemistry, such as nitrogen and major ions. With the presumption that the environment-species relationships have not changed over time, the preferences of different diatom species for these variables could be useful for the interpretation of the fossil diatom data in Bates Pond. For example, *Cyclotella stelligera* and *Fragilaria* spp. were most abundant in autumn and winter. Therefore, the increased abundance of these species in the fossil record between ca. 60 cm and 10 cm depth may indicate prolonged circulation periods and therefore generally cooler conditions. However, these taxa are indicators of human disturbance, too, such as discussed before. It is therefore important to determine the relative influence of climatic versus anthropogenic effects.

Intuitively, changes in diatom assemblages of a temperate lake would be interpreted in terms of nutrient availability, light conditions or pH. Temperature is more likely to influence ecosystems at climatic and vegetation boundaries (Smol and Cumming 2000). However, even if stratification and temperature are correlated with several other variables in our study site, they explain independently a significant amount of species variance in the trap samples. Also, there are some species that are correlated with stratification, but not with the second most important variable NO_3, such as *Asterionella ralfsii*. Other studies have shown that shifts in fossil diatom assemblages may indicate changes in seasonal mixing patterns induced by climate change (Bradbury 1988; Bradbury and Dieterich-Rurup 1993; Edlund et al. 1995).

The fossil samples from 10 to 30 cm (ca. 1830 to 1940 AD), which were plotted in ordination at the lower end of the temperature gradient (Fig. 5.6), correspond to the later part of a period of climatic cooling, the Little Ice Age (Bradley and Jones 1993). Cooler conditions around 1500 AD (Cronin et al. 2003) and during the 18th century, as well as wetter conditions during the 18th century (Cronin et al. 2000) were recorded in marine cores in Chesapeake Bay (Maryland), which belongs to the same climatic region. A study of diatoms in sediment traps and a sediment core in a Swiss alpine lake showed that *Fragilaria* spp. mainly enter the traps during winter and that a higher abundance of these species in the sediments corresponded to longer ice cover during the Little Ice Age (Lotter and Bigler 2000). In Bates Pond, *Fragilaria* spp. entered the sediment traps also during autumn and winter (Fig. 5.5). In the fossil record, their abundance increased by 5% in sediments dating from ca. 1050 to 1200 AD, remained stable until European settlement and increased more after settlement (Fig. 5.9). Furthermore, the taxon *Aulacoseira distans* var. *tenella,* which is negatively correlated with stratification and temperature, showed an increase in the pre-settlement sediments between 70 and 80 cm (ca. 1100 – 1300 AD) (Fig. 5.9). Therefore, the changes in diatom assemblages due to human influence from ca. 1700 AD to 1900 AD may have been initiated before settlement by climate-driven changes in the mixing regime of Bates Pond.

Interestingly, the decreasing temperature trend as inferred by the PLS model based on the trap samples began from the lowest core samples and continued until about 10 cm, whereas the inferred NO_3 changes occurred later (Fig. 5.10). Thus they support the hypothesis that assemblage changes were initiated before European settlement and have to be partly attributed to natural causes. Evidently, as the model is only based on 11 samples, which are not independent at a spatial and temporal scale, this result has to be viewed with much caution. For developing a statistically robust model and for conclusions about temperature/mixing preferences of individual species, investigations of one or more lakes over several years are needed, such as demonstrated by Hausmann and Pienitz (unpublished data).

Despite the presence of all dominant fossil species in the sediment traps, different relative abundances of some taxa created a distance between both fossil and modern sample sets in ordination (Fig. 5.6). This distance is partly due to the higher proportion of epipelic diatoms (*Navicula* spp.) in the fossil samples, which are concentrated in the surface sediments by sediment focusing, vertical transport and epipelic growth. These factors are likely constant through time and therefore do not affect the comparability of trap and core samples. However, also the high relative abundances of *Asterionella* spp. and *Nitzschia gracilis* during summer are not reflected in the sediments and relative abundances of *Cyclotella stelligera* were much higher in the sediments than in the trap. These differences may be caused by inter-annual variability in the seasonal cycle of the lake, indicating that at least one additional year of observations would be useful for testing the repeatability of our results.

Our study illustrates that ecological information is potentially encoded in the modern seasonal cycle of a lake, which may be used for interpretation of the fossil record of the same lake. This is particularly interesting for paleoclimatic studies in temperate regions, where ecotonal and climatic boundaries are difficult to find. Here, climatic change may result in more subtle ecosystem responses, such as changes in the seasonal lake dynamics. For the paleolimnological approach this means that, if a lake is chosen for a long-term record of environmental change, the knowledge of the present seasonal variability in biological paleoclimatic proxies, such as diatoms, may provide important information for the interpretation of fossil records.

The period of highest diatom abundance in Bates Pond was the autumn. This confirmed the general pattern in dimictic, temperate lakes of highest diatom abundances during spring and autumn overturn (Sommer et al. 1986). Consequently, the species with the closest correlation to the major environmental gradient in Bates Pond occurred also in autumn (Figs. 5.5 and 5.7), but the similar spring assemblages responded to similar environmental conditions. For the development of diatom-based inference models this implies that the highest correlation of the measured environmental parameters with the subfossil diatom sample exists during autumn and spring, which are therefore the most representative sample seasons. This finding confirms the results of previous studies. For example, the development of a diatom model based on spring TP in Danish lakes performed slightly better than the model based on mean annual TP (Bradshaw et al. 2002), whereas a robust TP model has been developed in Finland using autumnal TP (Kauppila et al. 2002). For Bates Pond, autumn appears to be the best time for relating diatom species to environmental variables; however, given the similarity of the spring samples and the general seasonal preferences of diatoms, spring may be equally appropriate in temperate, dimictic lakes.

It remains to be tested if seasonal patterns of the periphytic diatom assemblages follow similar timing and driving factors as the planktonic diatoms and what implications this may have for the selection of a sampling season for diatom model development. In our study, tychoplanktonic species dominated both the sediment trap and the fossil assemblages, despite the fact that the lake is shallow and has a large macrophyte cover in the littoral zone. Therefore, benthic diatom assemblages do not exert a major influence on the results of this study. As subfossil assemblages used for calibration sets and sediment cores for paleolimnological studies are usually taken in the deepest part of the lake, planktonic and tychoplanktonic species represent an important part of the fossil assemblages in most lakes. The seasonality of this component of the diatom assemblages should therefore determine the decision for chosing the sampling season. However, benthic diatom populations can dominate in small and shallow lakes. The ecology of lentic benthic algal communities is much less known than that of lake phytoplankton or lotic epiphyton (Lowe 1996). A study of a lake in England has shown that benthic diatoms reach maximum biomass in the spring (Talling 2002), indicating that also the benthic component may reflect spring conditions. Even if a better understanding is needed of the factors controlling seasonality in benthic diatom communities, it appears that spring and autumn rather than summer are the most appropriate seasons for taking water samples for diatom model development.

The results obtained here are probably applicable to a wide range of small temperate lakes, which are often chosen for inference model development and paleolimnological analysis because of their simple morphometry and sedimentation patterns. In North America, small, oligotrophic lakes represent a large part of the lake population, especially in boreal forest regions. Temperature is likely an important factor controlling seasonal patterns of diatom succession in many lakes and is therefore potentially useful to develop seasonal transfer functions. However, nutrient-rich lakes, which are more frequent in central Europe, are also strongly controlled by the seasonal availability of nutrients, which may be helpful for developing seasonal TP transfer functions.

5.8 Conclusions

With the study of a one-year seasonal sequence of diatoms and the fossil diatom record covering the last 1500 years in Bates Pond, Connecticut, the implications of seasonal diatom dynamics for paleolimnological analysis were assessed. The seasonal patterns in diatom assemblages were mainly related to changes in stratification and, to a lesser extent, to nitrate, silica, and phosphorus. During the full-circulation periods in spring and autumn, the richest diatom populations dominated by tychoplanktonic species developed and were only replaced by some lightly silicified, spindle-shaped planktonic diatoms during two months of thermal stratification in summer. Changes in fossil diatom assemblages likely reflected human activity in the watershed after European settlement and subsequent recovery in the last century. In addition, a long-term trend in diatom assemblage change initiated before European settlement was probably related to increased length of mixing periods during the Little Ice Age, such as indicated by the increase of taxa that presently grow during full circulation periods and by application of a preliminary seasonal temperature model. The study of limnological conditions and diatom succession in more similar lakes or over several years in one lake would be desirable in order to establish a more robust seasonal data set for the enhancement of paleolimnological interpretations. Also, the main part of diatom numbers has been deposited during autumn, whereas the spring assemblages were less numerous, but similar to autumn assemblages. This indicates that spring and autumn may be the best seasons for sampling of lakes with the purpose of developing diatom inference models in temperate, dimictic lakes. In conclusion, this study has shown that the investigation of seasonal diatom dynamics in temperate lakes may provide important information for the refinement of paleolimnological interpretations.

5.9 Acknowledgements

This study was supported by the National Science Foundation grant no. 9903792 attributed to D. Foster, and by the Natural Sciences and Engineering Research Council of Canada (NSERC) through an operating grant to R. Pienitz. Logistic support was provided by the Centre d'études nordiques, Québec, and Harvard Forest, Petersham. We thank Sylvia Barry for doing much of the field work. We are grateful to the Ginetti family for their friendly permission to access and study Bates Pond. We owe many thanks to S. Hausmann for fruitful exchange of ideas throughout the entire study period and comments on this manuscript. We acknowledge help in fieldwork by C. Zimmermann, S. Hausmann, K. Roberge, T. Menninger, and E. Faison. Water samples were analyzed in the National Laboratory of Environmental Testing, Burlington, Canada.

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6 Response of four New England lakes to climate change and human disturbance during the last ca. 1500 years: regional versus local factors

6.1 Résumé

Les résultats des analyses paléolimnologiques pour les derniers environ 1500 ans de quatre lacs en Nouvelle-Angleterre ont été synthétisés pour en tirer des conclusions générales sur l'histoire environnementale de la région. Tous les lacs ont enregistré clairement le patron régional de la perturbation anthropique suite à la colonisation européenne. Toutefois, la sensibilité aux changements climatiques avant l'arrivée des Européens, la façon de répondre à la perturbation et la capacité de récupérer après que la forêt se soit rétablie dans les bassins versants étaient plutôt contrôlées par les facteurs locaux, tel que la profondeur d'eau, la présence de marais dans le bassin versant, l'histoire des perturbations locales et la capacité de tampon. Des futurs études paléoécologiques visant à mieux définir les changements climatiques pendant le Petit Âge Glaciaire devraient adopter une approche pluridisciplinaire à haute résolution temporelle dans les lacs situés proche des limites écologiques, par exemple en altitude.

6.2 Introduction

In chapters 3, 4, and 5 the environmental histories of four New England lakes have been analyzed in detail, and the relative importance of natural and human factors for the individual lake development has been assessed. However, for inferring climatic trends and patterns in ecosystem response and recovery following human disturbance on a regional scale, it is necessary to assess to what extent the results from individual study sites can be generalized. Patterns that all sites have in common should indicate driving factors that act on a regional scale, such as climate or parallel regional historical development. Differing patterns would reflect local factors, such as catchment vegetation, lake morphology, altitude, timing of settlement, intensity and duration of human disturbance.

In an attempt to separate regional from local factors, the results obtained from paleolimnological analyses in the four New England lakes (chapters 3, 4 and 5) are comparing through addressing the following questions:

- Are there patterns that are common to all lakes and can such patterns be attributed to regional factors?
- To what extent do the lakes differ from each other and how can these differences be explained?
- What can be concluded from our results in terms of climate change before European settlement as well as lake response and recovery following human disturbance?
- What kind of information is missing to draw a general picture of the interplay between climatic and anthropogenic factors controlling New England lakes and how could this information be obtained?

6.3 Study sites and methods

The location of the four study sites in New England is illustrated in Fig. 6.1. For major lake characteristics, refer to Table 1.1.

Detrended correspondence analyses (DCA) with detrending by segments and non-linear scaling using the computer program CANOCO for Windows 4.0 (ter Braak and Šmilauer 1998) showed that all fossil data sets had a total variance smaller than two standard deviations, and hence, linear methods were applied in further data analyses (Birks 1995). In order to summarize the patterns in diatom assemblage composition, principal component analyses (PCA) on a covariance matrix were carried out. The change in fossil diatoms which explains the major part of variance and therefore reflects the major direction of change is represented by PCA axis one, while the second most important change is described by PCA axis two. Procedures applied for diatom and LOI analyses are detailed in chapters 3, 4, and 5. For quantitative reconstructions, the method of weighted averaging (WA) with inverse deshrinking and square-root transformation of species data was used for pH, whereas Gaussian logit regression (GLR) with untransformed abundance data was used for total phosphorus (TP).

Core chronologies were established by radioisotopes ^{210}Pb, ^{14}C, and pollen settlement horizons, as well as linear interpolations between the oldest ^{210}Pb date, the settlement date and the ^{14}C dates, such as described in chapters 3 (Walden Pond), 4 (Levi Pond and North Round Pond), and 5 (Bates Pond). In order to compare the lakes' histories in the context of natural and human disturbances, we present and discuss the results with reference to these chronologies.

Figure 28 Location of the four study sites in New England.

6.4 Results and discussion

The results of the paleolimnological analyses carried out on the sediments of Walden Pond (Massachusetts), Bates Pond (Connecticut), North Round Pond (New Hampshire) and Levi Pond (Vermont) are summarized in Fig. 6.2. The result are discussed following the order of the four major periods of human civilisation in north-eastern North America: the Native American, the Colonial, the Industrial and the Post-industrial period.

6.4.1 Native American (Pre-settlement period, until 1600 AD)

The length of the record available for the pre-settlement period differs between the four lakes, with the longest record being analyzed for Levi Pond, Vermont (since 400 BC), and the shortest record for Bates Pond, Connecticut (since 800 AD), although the shortest sediment sequence was analyzed in Levi Pond. The low sedimentation rate in Levi Pond is exceptional amongst our study sites and is likely due to its oligotrophic and acidic nature.

In general, the analyzed proxies did not show any striking changes before settlement, but some gradual, long-term trends in all lakes, except for Walden Pond. These long-term trends differed between lakes in nature and timing. The trend in diatom assemblages in Bates Pond, starting from ca. 1100 AD and continuing into the settlement period until ca. 1850 AD (Fig. 6.2 b, PCA axis 1), corresponds to a slight increase in diatom-inferred pH and probably reflects an increased length of full circulation periods as inferred from the recent seasonal distribution of diatoms in the same lake (chapter 5). In North Round Pond, the PCA axis 1 indicates a trend from the bottom of the core (ca. 500 AD) continuing until the Colonial period. It corresponds to a slight increase of diatom-inferred TP concentrations and is also expressed by decreasing abundances of planktonic diatoms (Fig. 6.2 c), probably indicating gradual lake infilling and increased aquatic productivity. These patterns may be part of natural processes of lake evolution, but may also have been enhanced by natural disturbance. Increased fire frequency, such as indicated by increased charcoal : pollen ratios and increased abundance of fire-resistant tree species at North Round Pond starting ca. 1200 AD (Francis and Foster 2001), may have enhanced nutrient transport to the lake and thereby accelerated lake infilling and nutrient enrichment.

In contrast to North Round Pond, the planktonic species in Levi Pond increased over the last ca. 2000 years, also expressed by PCA axis 1 and increased diatom-inferred DOC (Fig. 6.2 d). Correlations with stable isotope and pollen data and an increase of the cold-water chironomid genus *Microtendipes* from the same pond indicate that this long-term trend in diatom assemblages reflected a long-term humidity increase associated with Neoglacial cooling (chapter 4). As this trend started around 0 yr AD, the absence of analyzed samples dating before ca. 500 yr AD for the other three lakes may be one reason why no such change was observed there. However, the presence of a wetland in the watershed makes Levi Pond also special amongst the study lakes. Therefore, more long-term diatom records from New England lakes would be necessary to test the hypothesis that lakes in this region have responded to Neoglacial cooling that was accompanied by changes in the hydrologic regime.

Another potential impact on New England ecosystems before European settlement may derive from Indian activities. There is historical evidence that the autochthonous populations in New England cleared some forest for villages and fields and set fires for hunting and for facilitating travel (Day 1953). However, their activities were mainly restricted to the coastal region and large river valleys, and to date there is no comprehensive record of the modification of the New England Forests brought about by the Indian population (Foster 1995).

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Short-term events associated with climate change during the Little Ice Age were not identified by our diatom analyses. The hypothesis of longer full-circulation periods from ca. 1100 AD to 1800 AD at Bates Pond has to be tested through additional paleolimnological records in that region and a more thorough study of the seasonal diatom succession. Chironomid analyses showed increased abundances of the cold water genus *Microtendipes* from 1200 AD to 1800 AD at North Round Pond, but many other New England lakes did not provide evidence for climatic cooling (Donna Francis, personal communication). As the culminating period of the Little Ice Age occurred during the 18th and 19th centuries in North America, climatic signals were probably obscured by effects of human disturbance. Also, the climate change before 1700 AD may not have been substantial enough to affect diatom assemblages in this region. The studied environmental gradients did not include any ecotonal boundary, where a sensitive response of aquatic organisms to small-scale climatic change would be more pronounced (Smol and Cumming 2000). Alternatively, climate cooling during the Little Ice Age may have been less evident in New England than in other regions.

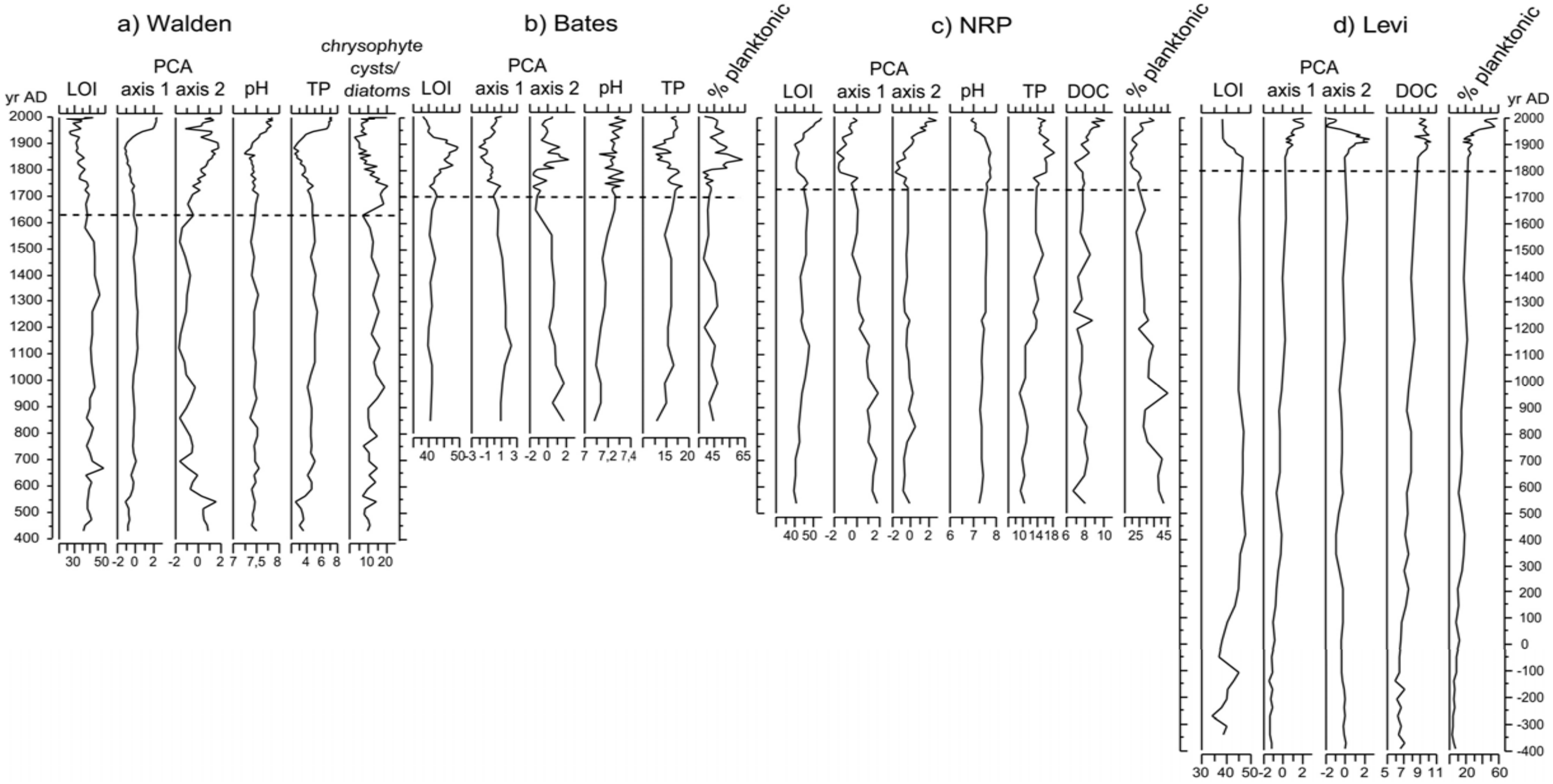

Figure 29 Summary of paleolimnological analyses of four New England lakes.
a) Walden Pond, b) Bates Pond, c) North Round Pond and d) Levi Pond. PCA = sample scores on axis 1 and 2 resulting from principal components analyses of fossil diatom samples, LOI = loss-on-ignition, TP = diatom-inferred total phosphorus in $\mu g\ l^{-1}$, DOC = diatom-inferred dissolved organic carbon in mg l^{-1}. Horizontal dotted lines indicate the settlement dates for each lake.

It is also possible that the temporal resolution of our analyses was not fine enough for detecting climate events on a multi-decadal scale, which were associated with the Little Ice Age (Clark 1990; Bradley and Jones 1993). While our analyses from 1700 AD to the present were carried out at average resolutions of 1 or 2 cm intervals representing 13, 11, 18, and 19 years for Bates, Walden, North Round, and Levi Pond, respectively, the resolutions for the period from 1200 AD to 1700 AD were 80 (4 cm intervals), 60 (2 cm intervals), 70 (2 cm intervals) and 220 years (2 cm intervals) for Bates, North Round, Walden and Levi Pond, respectively. As the sedimentation rates before settlement were low, analyses at a minimum interval of 0.5 cm for this period would be necessary to resolve environmental changes at the multi-decadal scale. Additionally, the Little Ice Age coincides with the gap between the oldest ^{210}Pb and the youngest ^{14}C dates, which complicates the establishment of a precise chronology for that period.

In summary, the four study lakes did not exhibit any similar pre-settlement pattern, indicating that diatom assemblages in the study lakes were not primarily controlled by a common regional factor, such as climate change, during the last ca. 1500 years. Rather local processes and events such as individual lake evolution and natural disturbances determined the pre-settlement dynamics in these lakes. The long-term increase in humidity during the last ca. 2000 years inferred from Levi Pond sediments was not detected in the other lakes, probably because of shorter records. Drawing a regional picture of the timing and nature of climate change related to the Little Ice Age in New England remains a challenge due to the complex combination of factors controlling the lakes, such as natural disturbances, long-term ecosystem development, interfering human disturbances and local lake features, as well as the scarcity of ecotonal boundaries that represent climatic limits for indicator organisms. This challenge may possibly be addressed with a multi-proxy, high-resolution paleolimnological study of lakes at higher elevation, such as in the White Mountains, New Hampshire, which ideally should not have experienced any major historical or natural disturbance in the watershed.

6.4.2 Colonial (ca. 1600-1840 AD)

European settlers arrived at different times at the lakes, first at Walden Pond around 1630 AD, then at Bates around 1700 AD, afterwards in the region of North Round Pond (ca. 1730 AD), and at latest (around 1790 AD) at the pond at the highest elevation and farthest from the coast, Levi Pond. Diatom assemblages in all lakes responded to human activities in the watersheds, such as logging (Walden Pond, North Round Pond, Levi Pond) as well as extensive agriculture (Bates Pond). However, no major quantitative changes in lake characteristics were inferred, with the exception of an initial TP increase in North Round Pond. This TP increase correlates also with increased abundances in chironomid taxa that are typical of productive lakes (Francis and Foster 2001). While organic matter decreased in Walden Pond, Levi Pond and North Round Pond sediments, probably due to increased erosion of the soils in the watershed, it increased at Bates Pond where the large watershed and the more intensive land use (agriculture) may have contributed to more organic matter inputs into the lake. Our findings are similar to changes in sediment composition and diatom assemblages that have been observed in other New England lakes due to moderate land use following settlement (Brugam 1978; Davis and Norton 1978; Engstrom et al. 1985).

Interestingly, the long-term trends observed during the pre-settlement period, such as the diatom trends described by PCA axes 1 in Bates Pond, North Round Pond and Levi Pond, continued or accelerated after settlement. For example, the gradual increase of benthic taxa at North Round Pond, probably related to lake infilling, continued after settlement and was accelerated by logging in the watershed. At Bates Pond, the trend in diatom assemblages that is probably caused by longer full-circulation periods, also continues until the mid-19th century and was intensified by the opening of the landscape due to forest clearance. Apparently, natural lake evolution processes and climatic factors continued to influence the lakes during the Colonial period.

Overall, the first human influences during the Colonial period seem to have affected the lake ecosystems to a minor degree, and natural processes still seem to have driven to lake development. There is regional evidence of human impact on the lakes, but the response of the lakes differed by the timing of settlement, the nature of sediment composition change and the changes in species composition regarding habitat preferences, depending on lake location, disturbance intensity and lake morphology.

6.4.3 Industrial (ca. 1840-1960)

During the most intensive land use period in New England with intensive agriculture and the highest population growth and densities in the countryside, the majority of the lakes exhibited the largest changes within the study period, but also started to recover after abandonment of agricultural land due to migration to urban centres. Organic matter content continued the trends that had started during the Colonial period and attained their maximum values at Bates Pond, yet reached minimum values at North Round Pond, Levi Pond and Walden Pond. The assemblage changes associated with settlement in Walden Pond and Levi Pond (PCA axes 2) reached their highest deviation from background values around 1900 AD and reversed afterwards, closely tracking the period of highest human activity in the watershed and subsequent land abandonment. The highest proportion of planktonic taxa at Bates Pond related to increased exposure to wind after opening of the landscape and probably to nutrient enrichment by agricultural activities in the watershed that occurred around 1850 AD and decreased afterwards, when the catchment vegetation started to recover. In contrast, the planktonic taxa at North Round Pond reached minimum values caused by increased macrophyte abundance likely following lake infilling and nutrient enrichment, but started to increase from ca. 1900 AD onwards. Diatom-inferred TP reached maximum values in North Round Pond, DOC increased in Levi Pond and TP and pH started to increase in Walden Pond, indicating increased input of organic matter, nutrients and minerals from the watersheds. Such trends in altered water chemistry due to intensive land use have been inferred for many New England lakes with the help of diatom transfer functions (Davis et al. 1994; Dixit et al. 1999; Siver et al. 1999).

By the end of this period, about 1960 AD, most lakes were still changing, except for Bates Pond, which had reached approximately the same state that it had when European settlers arrived. The trends in water chemistry did not reverse after reforestation, except from a small decrease of TP in North Round Pond. However, at North Round Pond, LOI and diatom-inferred DOC increased from ca. 1930 onwards, likely as a result of a major hurricane that destroyed large parts of the watershed vegetation. At Walden Pond, recreational activities had begun in the early 20th century, and therefore a new type of disturbance started to profoundly affect this lake despite complete reforestation of the watershed. This has left a distinct signature in the fossil diatom record and in the stable isotope composition (chapter 3). The diatoms that were related to watershed disturbance at Levi Pond had almost disappeared by the mid-20th century (chapter 4), but the new-formed assemblage was dissimilar to that observed before settlement, as discussed below.

In summary, the diatom assemblages responded sensitively to the human activities in the lake watersheds related to the regional maximum of land clearance and population densities in the countryside of New England during the mid-19th century. Changes in lake water chemistry were reconstructed quantitatively for all lakes except Bates Pond. Diatom assemblages reflected also to some extent the starting recovery of the lake ecosystems due to land abandonment following migration to the industrial centres. However, despite the complete recovery of the vegetation by 1960 AD, such as suggested by pollen analyses and lake surveys, three of four lakes have not entirely returned to the pre-settlement conditions. These fossil records obtained from the aquatic ecosystems substantiate the statement that land use during the Colonial period was an intensive regional disturbance for the New England forests (Foster et al. 1998).

6.4.4 Post-Industrial (1960-present)

During the second half of the 20th century, the lakes showed the most obvious divergence in their individual development. While Bates Pond had recovered from the human disturbance by 1930 AD and appeared to have stabilized, Walden Pond, North Round Pond and Levi Pond seem to undergo a new direction of lake development. The most evident change during the post-industrial period has occurred in Walden Pond during the last 80 years, where the intensive recreational use of a beach and trails in the watershed resulted in eutrophication, such as a substantial change in diatom assemblages, increased diatom-inferred TP and pH, a shift in chrysophyte assemblages to nutrient-tolerant species and changes in stable isotope composition that are all typical signs for nutrient enrichment of lakes (Chapter 3). In North Round Pond, the diatom assemblage changes, decreasing diatom-inferred pH, as well as rising diatom-inferred DOC and sedimentary organic matter initiated after the major hurricane in 1937 and continuing until the present day and may be associated with progressive lake shallowing due to enhanced sediment input from the disturbed watershed and delayed recovery from acidification (chapter 4). In Levi Pond, a new diatom assemblage has formed in the mid-20th century, and DOC and LOI did not return to pre-settlement values, indicating that other factors still contribute to this lake's development, such as humidity-driven peatland expansion and probably acidification. Surface water acidification following atmospheric deposition, such as recorded in many lakes in New England (Likens et al. 1996) and the close Adirondacks (e.g. Charles 1990; Smol and Dixit 1990; Cumming et al. 1994) was only observed in North Round Pond, and possibly in Levi Pond. On the other hand, the mesotrophic Walden Pond and Bates Pond seemed to have sufficient buffering capacity (acid neutralizing capacity = ANC) to be relatively insensitive to acidification, which has been shown for Connecticut lakes (Siver et al. 1999; Siver et al. 2003).

These results provide evidence that, despite the reforestation of watersheds in New England by the mid-20th century, several ponds have not returned to pre-settlement conditions, because they are still influenced by recent watershed disturbances and peatland development. Their recovery capacity appears to depend largely on local site characteristics, such as ANC, lake depth and local disturbance history. Therefore, restoration efforts focussing on the re-establishment of pre-settlement conditions may not always be appropriate, because lake evolution may reach new, irreversible states (such as in North Round Pond and Levi Pond). On the other hand, present-day threats, such as atmospheric acidic deposition (such as in North Round Pond) and human-induced eutrophication (such as in Walden Pond) can be avoided and reversed by political and management measures.

The preservation of the "natural state" of Bates Pond was partly the result of its buffering capacity and absence of natural disturbance, but would not have been possible without the protection from major anthropogenic influences by its proprietors during much of the 20th century. It may therefore serve as an example for the possible recovery of surface waters that have historically undergone human impact.

6.5 Conclusions

The comparison of limnological changes in four New England lakes during the past ca. 1500 years has shown that all aquatic ecosystems responded markedly to regional patterns in human disturbance during the Colonial and Industrial periods, but that local site factors had a strong control on natural lake evolution before human settlements, the nature of response to the disturbance and the extent of recovery after reforestation of the watersheds. Increased humidity related to the Neoglacial cooling during the past 2000 years caused a long-term increase in DOC concentrations at Levi Pond, but was not evident in the other lakes, probably due to the shorter sedimentary records or the absence of wetlands in the watersheds. Short-term climatic events, such as the Little Ice Age, have not left any clear signal in the stratigraphies, likely due to obscuring effects of human disturbance, insufficient magnitude of changes and/or insufficient sample resolution. However, the diatom assemblages responded sensibly to the human activities in the lake watersheds related to the regional maximum land clearance and population densities in the countryside of New England during the mid-19th century, but also continued to respond to climatic factors and lake evolution processes. Despite the reforestation of watersheds in New England by the mid-20th century, three out of four lakes have not returned to pre-settlement conditions, because their local site characteristics make them susceptible to past or recent watershed disturbances, acidification and climate change.

Apparently, climate played a minor role in the past dynamics of the aquatic ecosystems studied here. This underlines the difficulty of detecting past climatic variations using biological proxies in temperate regions, where temperature is not the dominant limiting environmental factor for most populations. Future paleoecological studies aiming at elucidating the timing and nature of climate change related to the Little Ice Age in New England should use a high-resolution, multi-proxy, multi-site approach near ecotonal boundaries, such as high altitudes, in order to disentangle the complex processes that control lake development in this region.

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7 Conclusion générale

Les recherches effectuées dans le cadre de cette thèse représentent une contribution nouvelle aux connaissances sur l'évolution des lacs en Nouvelle-Angleterre avant et après la colonisation Européenne de la région. De plus, deux aspects méthodologiques nouveaux et pertinents pour la discipline de la paléolimnologie ont été développés.

Un aspect novateur de nos travaux est l'application de la méthode des réseaux neuronaux artificiels pour la reconstitution quantitative des variables environnementales à partir des diatomées fossiles. La pertinence de son emploi pour cette fin a été démontré (chapitre 2). Dans un même temps, la révision et l'amélioration de certaines méthodes classiques et des transformations fréquemment utilisées en paléolimnologie devrait permettre aux chercheurs en ce domaine de tirer des informations quantitatives plus fiables de leurs données.

L'étude paléolimnologique du lac Walden Pond (chapitre 3), qui représente un site historique important et populaire, a démontré que l'usage récréatif a causé une eutrophisation rapide du lac depuis le début du 20e siècle. La mise en évidence d'une stabilisation récente de son état suggère que des mesures de gestion entreprises dans les années 1970 ont freiné la tendance vers une eutrophisation continue. De plus, avec la caractérisation de son état naturel nous avons fourni des informations essentielles pour la restauration du lac.

Les effets de la perturbation anthropique dans le contexte des changements climatiques ont été étudiés dans plusieurs lacs en Nouvelle-Angleterre. Nos résultats montrent que les quatre lacs étudiés ont enregistré clairement un patron régional propre à la perturbation anthropique suite à la colonisation Européenne (chapitres 3, 4, 5 et 6). Ceci confirme les résultats des études faites antérieurement. Toutefois, l'évolution naturelle des lacs, les perturbations naturelles ainsi que le climat ont également influencé le développement des lacs pendant la période coloniale. Ces facteurs, couplés avec les caractéristiques locales des sites, ont aussi fait en sorte que parmi les quatre sites d'étude, trois montrent encore à l'état actuel des conditions qui ne correspondent pas à celles de la période avant-perturbation. Ces lacs ont plutôt atteint un nouveau stade limnologique dans leur évolution. Ces résultats indiquent que l'état du lac avant la perturbation ne correspond pas nécessairement à l'état « naturel » théorique envisagé, bien que ce soit souvent un guide d'orientation pour les mesures de gestion. Il est donc important de tenir compte de l'évolution naturelle des lacs et des impacts climatiques pour établir des objectifs de restauration réalistes.

Des changements climatiques de relativement courte durée, tel qu'associés avec le Petit Âge Glaciaire, n'ont pas été identifiés de façon claire dans nos lacs. Ceci est probablement dû aux effets camouflant de la perturbation anthropique, à une amplitude insuffisante des changements climatiques pour avoir affecté des populations aquatiques et/ou à une résolution temporelle des analyses trop faible. Une explication alternative pourrait être que le Petit Âge Glaciaire n'a pas été aussi prononcé en Nouvelle-Angleterre que dans d'autres régions du monde. Toutefois, dans Levi Pond au Vermont, une tendance à l'humidité accrue pendant les dernières 2000 années, qui correspondait au refroidissement global du Néoglaciaire, a été indiquée par la composition des assemblages de diatomées. Ce résultat est un nouvel indice que les diatomées sont d'une utilité potentielle pour les études paléohydrologiques dans les régions tempérées.

Notre étude de la succession saisonnière récente des diatomées à l'aide des pièges de sédiment dans le lac Bates Pond s'est avérée utile pour l'approfondissement de l'interprétation des séquences fossiles des diatomées (chapitre 5). En premier lieu, une augmentation dans le passé de l'abondance relative des espèces qui sont aujourd'hui associées avec le mélange entier de la colonne d'eau a indiqué une durée de mélange prolongée dans le passé. En deuxième lieu, le maximum de productivité diatomifère en automne indique que c'est la saison privilégiée pour l'échantillonnage d'eau en vue du développement des fonctions de transfert élaborées à partir des diatomées. Ces résultats ouvrent de nouvelles pistes à suivre pour peaufiner les interprétations des enregistrements paléolimnologiques et pour améliorer des fonctions de transfert.

Plusieurs nouvelles hypothèses établies ici devraient être soumis à des tests au cours de futurs études. L'utilité des réseaux neuroneaux artificiels pour les reconstitutions quantitatives à partir des diatomées et d'autres indicateurs paléoécologiques, comme les chironomides et les pollens, est à évaluer par le biais d'autres ensembles de données récentes et fossiles. Le potentiel des diatomées pour les études paléohydrologiques via les variations dans les concentrations du carbone organique dissous reconstitué sera à vérifier dans d'autres lacs. Afin de compléter l'interprétation des assemblages fossiles, l'étude de la dynamique saisonnière des diatomées et d'autres algues utilisées en tant qu'indicatrices paléoécologiques est recommandée dans les lacs qui sont choisis pour l'étude paléolimnologique. Ceci est surtout valide pour les études paléoclimatiques dans les régions tempérées, où les changements climatiques ont des effets plus subtiles sur les populations aquatiques que dans les régions de haute latitude.

Dans de futurs études paléoécologiques qui visent à déterminer de façon plus précise le cadre temporel, le caractère et l'amplitude des changements climatiques liés au Petit Âge Glaciaire en Nouvelle-Angleterre, on devra essayer d'exclure des processus qui camouflent le signal climatique et tenter d'identifier les variations de courte durée. Pour ce faire, on devra adopter une approche pluridisciplinaire à haute résolution dans plusieurs sites proche des limites écologiques des organismes, tel qu'en haute altitude, et qui n'ont idéalement pas subit de perturbations anthropiques et naturelles majeures dans leurs bassins versants.

Appendice: Results of ^{210}Pb dating

Walden Pond

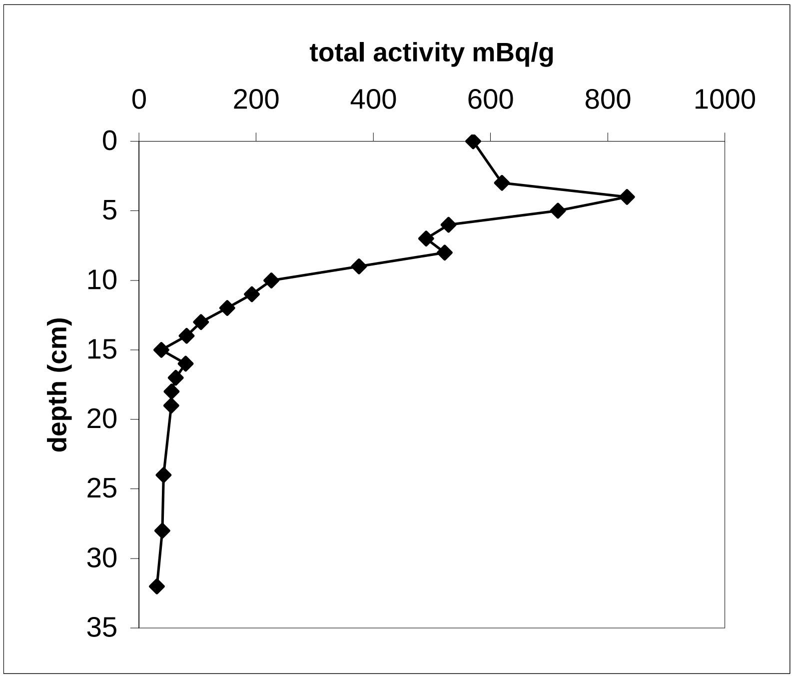

Fig. A.1. Total ^{210}Pb activity versus core depth for Walden Pond, Massachusetts.

Levi Pond

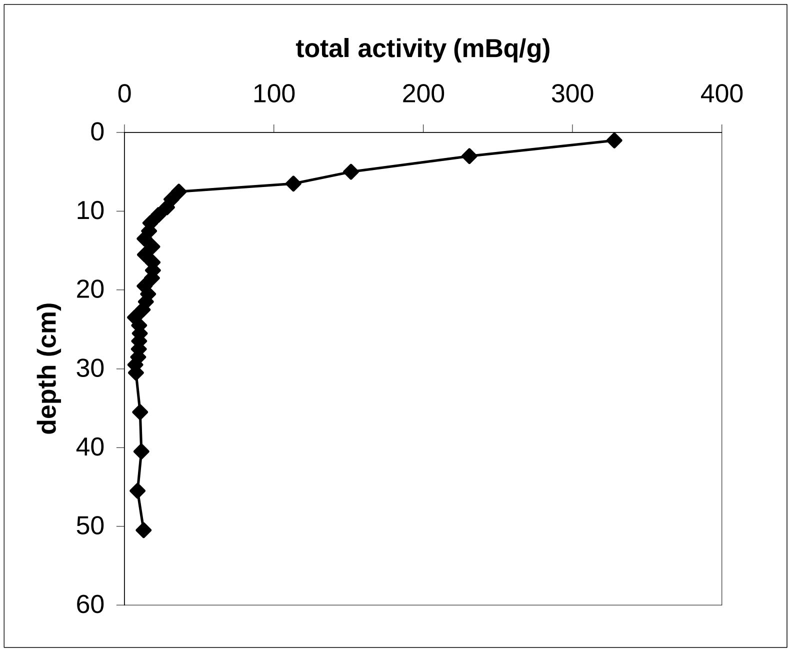

Fig. A.2. Total ^{210}Pb activity versus core depth for Levi Pond, Vermont.

North Round Pond

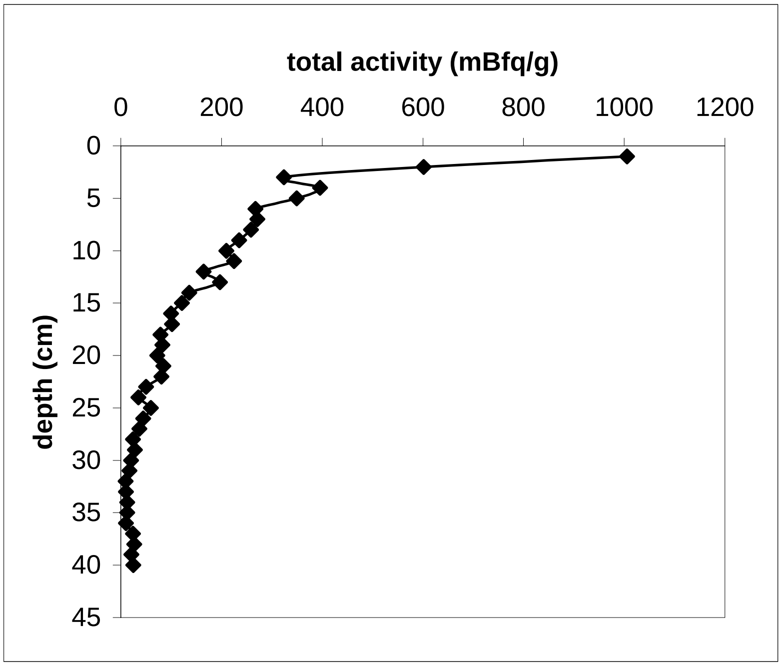

Fig. A.3. Total ^{210}Pb activity versus core depth for North Round Pond, New Hampshire.

Bates Pond

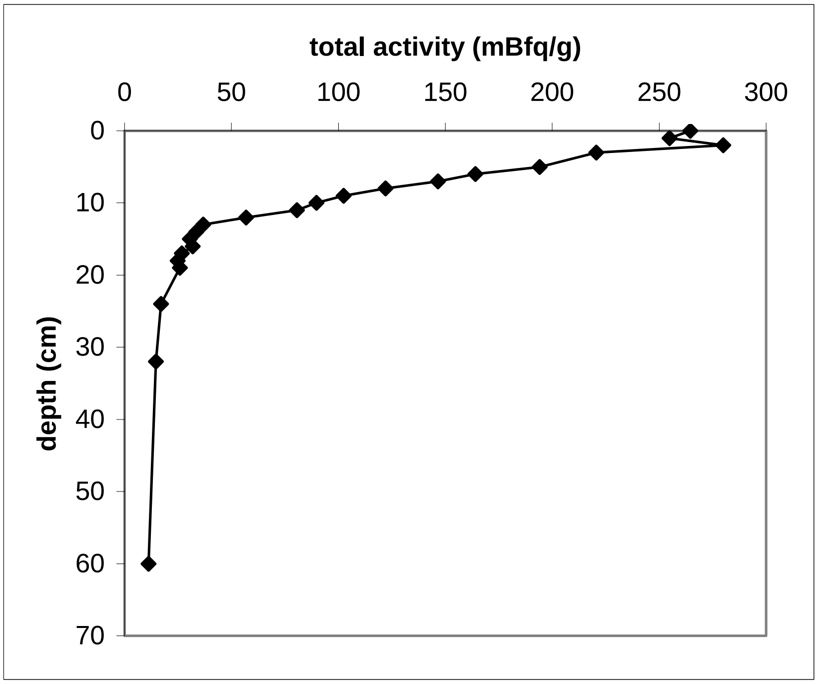

Fig. A.4. Total ^{210}Pb activity versus core depth for Bates Pond, Connecticut.