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Effets de la coupe forestière et des feux de forêt sur la structure des communautés zooplanctoniques des lacs du Bouclier boréal canadien

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Effets de la coupe forestière et des feux de forêt sur la structure des communautés zooplanctoniques des lacs du Bouclier boréal canadien

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Sommaire

Cette thèse s'inscrit dans le cadre d'un programme de recherche à l'échelle du Canada qui cherche à évaluer les effets des coupes forestières et des feux de forêt sur les écosystèmes aquatiques. Les coupes et les feux représentent deux importants facteurs de perturbation de la forêt boréale canadienne, les premiers d'origine anthropique, les derniers d'origine naturelle. Bien que ces deux perturbations ravagent chaque année de grandes étendues de forêt, leurs effets sur les écosystèmes lacustres demeurent en grande partie inconnus. Le but de cette thèse est de déterminer si la structure des communautés zooplanctoniques des lacs de la Haute-Mauricie (Québec) est affectée par la coupe forestière et les feux de forêt. La structure des communautés zooplanctoniques dépend de facteurs abiotiques (qualité de l'eau) et biotiques (biovolume du phytoplancton, densité de poissons zooplanctivores). Un changement induit par les coupes ou les feux dans un ou plusieurs de ces éléments devrait, en principe, se traduire par une altération de la structure des communautés zooplanctoniques.

Nous avons examiné la structure des communautés zooplanctoniques sous trois angles fondamentalement différents: biomasse, assemblage d'espèces et structure en taille. Nous avons comparé la structure des communautés zooplanctoniques dans trois groupes de lacs caractérisés par différentes conditions de bassins versants: un premier groupe de lacs dont les bassins versants ont été déboisés par la coupe à blanc, un deuxième groupe de lacs dont les bassins versants ont été brûlés par les feux de forêt naturels et un troisième groupe dont les bassins versants étaient intacts. Les coupes et les feux ont eu lieu pendant l'année 1995. L'étude de la structure des communautés zooplanctoniques s'est déroulée pendant les trois années suivant les perturbations des bassins versants. Trois méthodes d'analyse ont permis la caractérisation des échantillons de zooplancton: l'analyse taxonomique (pour la biomasse et les assemblages d'espèces); la détermination des poids secs dans quatre classes de taille obtenues par tamisage séquentiel du matériel planctonique

(pour la biomasse et la structure grossière en taille); l'analyse par compteur optique de particules (pour la biomasse et la sturcture fine en taille des crustacés).

D'après l'ensemble des résultats, la structure en taille des crustacés semble l'indice le plus sensible aux coupes et aux feux comparativement à la biomasse ou aux assemblages d'espèces. Les lacs aux bassins versants coupés et brûlés étaient en effet caractérisés par une plus grande dominance des organismes de grande taille, de telle sorte que la biomasse des grands crustacés (supérieur à 1 mm en diamètre sphérique équivalent) était trois fois plus élevée dans les lacs aux bassins versants coupés ou brûlés que dans les lacs de référence. D'autre part, la biomasse du plancton de taille 100-200 µm (algues, rotifères, nauplii de copépodes) était environ deux fois plus importante dans les lacs aux bassins versants brûlés. À l'inverse, la biomasse totale du zooplancton ne différait pas entre les lacs aux bassins versants perturbés et les lacs de référence (moins de 20% de différence). La décomposition de la biomasse totale en quatre grands groupes taxonomiques a permis de montrer que les calanoïdes étaient particulièrement sensibles aux coupes. Finalement, les assemblages d'espèces étaient naturellement trop variables pour servir d'indicateurs de perturbations du bassin versant. Dans l'ensemble, les feux ont eu un impact plus marqué sur la structure des communautés zooplanctoniques que les coupes. Cette différence tient probablement du fait que les feux ravageaient généralement des superficies de bassin versant deux fois plus grandes que les coupes; les changements dans la qualité de l'eau étaient également plus grands dans le cas des feux. Les résultats font également ressortir que les effets des perturbations du bassin versant sur la biomasse du zooplancton ne sont plus notables après trois années. Les importantes variations mensuelles dans la structure des communautés zooplanctoniques s'ajoutent aux variations naturelles entre lacs et limitent ainsi l'usage du zooplancton comme bio-indicateur de perturbations de bassins versants. Dans l'ensemble, les coupes forestières semblent entraîner une augmentation de la biomasse des crustacés de grande taille. Même si cette augmentation est moindre que celle qu'entraînent les feux, elle accompagne néanmoins des changements dans d'autres composantes de l'écosystème aquatique (chimie de l'eau, communautés de poissons), dénotant ainsi une véritable perturbation environnementale. Face à l'expansion sans cesse croissante des activités forestières au Canada, il y a lieu de continuer à surveiller les répercussions des coupes forestières sur les écosystèmes aquatiques.

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Je dédie cet ouvrage à ma grand-mère, Gabrielle Paquette Patoine, mes parents, Claude Patoine et Lorraine Lawrence Patoine, ainsi qu'à ma soeur Isabelle.

Avant-propos

Avant d'entreprendre cette thèse, je travaillais comme agent technique dans le secteur des biotechnologies environnementales de l'Institut de recherche en biotechnologie du CNRC. Pendant deux années j'ai vu au déroulement d'un projet de recherche portant sur la performance de diverses boues bactériennes anaérobies sur la dégradation d'une série de molécules toxiques contenues dans les effluents papetiers (les acides résiniques). Ce projet était tout à fait en ligne avec le projet de maîtrise que je venais de compléter à l'Université du Québec à Chicoutimi. Mes activités à l'Institut comprenaient la conception et le montage de bio-réacteurs de verre; leur ensemencement avec des boues échantillonnées dans des contrées aussi lointaines que Châteauguay; leur alimentation avec des solutions préparées d'acides résiniques; le dosage des ces acides, et le calcul de bilans massiques. Mon travail dans la salle des réacteurs alternait avec des lectures, des conférences et la rédaction d'articles. En résumé, je faisais ce que j'aimais: de la recherche.

Pendant mon séjour à l'Institut, je me voyais toutefois de plus en plus confiné à des problèmes de chimie analytique ou de dynamique des fluides. Je m'éloignais ainsi des aspects qui m'intéressaient le plus, à savoir ceux liés à la biologie, qui étaient, dans ce cas, la croissance et la composition en espèces des communautés bactériennes. Je voulais aussi retrouver la plus grande liberté de recherche des universités. En entreprenant cette thèse de doctorat, je renouais avec les concepts d'écologie que j'avais appris lors de mon B.Sc. à McGill. En m'intéressant à la façon dont les communautés aquatiques *réagissent* face aux activités de l'industrie forestière, j'adoptais une vue opposée à celle qui – dans mes travaux à l'Institut – consistait à *manipuler* une communauté dans le but d'amoindrir un des effets des activités forestières. Pendant cette thèse, j'ai profité d'un *enseignement* des méthodes d'analyse statistique des données, enseignement qui m'a permis d'étudier les questions qui m'intéressent. L'interprétation des données dans un cadre écologique est toutefois restée un travail essentiellement autodidacte, et ce, malgré les échanges et les conférences. Peut-on envisager l'enseignement d'une *méthode* qui vise à l'interprétation écologique des données? Ou bien les situations rencontrées en écologie sont-elles si différentes et si complexes que seules l'expérience, et peut-être une bonne intuition, peuvent départager une bonne d'une moins bonne interprétation écologique?

Introduction générale

La forêt boréale canadienne joue, depuis les débuts de la colonisation de l'Amérique, un rôle économique important. D'abord le lieu d'une importante traite des fourrures, la forêt boréale est ensuite devenue, vers la fin du XIXème siècle, la principale source de bois de l'industrie des pâtes et papiers (Centre Saint-Laurent, 1991). Aujourd'hui, l'industrie forestière rapporte plus à l'économie du Canada que les industries agricole, minière et piscicole combinées (Forestry Canada, 1991). Avec un développement sans cesse croissant, elle n'est toutefois plus perçue uniquement comme un moteur économique, mais aussi comme un facteur de perturbation de l'écosystème forestier qui peut nuire non seulement à la pérénité de la ressource en bois, mais également à la faune et à la flore qui s'y développent. Ce changement de perception suscite de nombreux questionnements dont témoignent, entre autres, le récent film «L'erreur boréale» (Desjardins et Mondrie, 1998), ainsi que la réforme du régime forestier québécois amorcée en 1996 (et dont la Commission parlementaire a clôturé le 26 octobre 2000). Voilà donc un sujet dont l'actualité ne saurait cacher une véritable et complexe problématique. Mais qu'en est-il du zooplancton? Quel rapport peut-il bien exister entre la coupe forestière et le zooplancton?

Aucun, si l'on considère que les lacs et les forêts sont des entités écologiques distinctes évoluant parallèlement, sans aucune influence de l'une sur l'autre. En fait, c'est de cette façon qu'a débuté l'étude des lacs au début du siècle (Wetzel, 1983: 134); très peu d'attention était alors accordée aux caractéristiques du terrain qui draine les eaux de pluie vers le lac (le bassin versant). À partir des années cinquante, on a commencé à étudier l'influence de certaines caractéristiques du bassin versant sur les communautés aquatiques (Huet, 1949 cité dans Allan & Johnson, 1997). De nombreuses études effectuées à partir des années soixante-dix ont démontré que les caractéristiques chimiques et biotiques d'un lac sont en partie dépendantes des caractéristiques du bassin versant (Schindler, 1971; Dillon & Kirchner, 1975). En effet, une fraction variable de la matière particulaire et dissoute d'un lac provient du bassin versant. En temps normal, un couvert forestier assure l'absorption des éléments nutritifs du sol et leur stockage dans les tissus arbustifs, en même temps qu'il agit comme une pompe qui retourne à l'atmosphère par évapotranspiration jusqu'à 90% du volume d'eau tombé en précipitations. On comprend dès lors que la perte d'un couvert forestier puisse avoir d'importantes répercussions sur le cycle hydrologique et sur la capacité d'un terrain à retenir ses éléments nutritifs. Ainsi, l'apport en phosphore et en azote d'un bassin versant à un lac est plus important dans le cas d'un bassin versant déboisé par rapport à un bassin versant non perturbé (Dillon & Kirchner, 1975; Lamontagne *et al.*, 2000). Le déboisement – par la coupe ou les feux – peut donc influencer la qualité chimique de l'eau.

Le zooplancton

Le zooplancton représente un groupe varié d'animaux qui peuple la colonne d'eau d'à peu près tous les plans d'eau, des étangs aux océans. Le zooplancton lacustre comprend des représentants des rotifères, les plus petits animaux connus (classe des Aschelminthes), des cladocères et des copépodes (classe des Crustacés, ordre des Arthropodes). La taille de ces organismes varie de 0,1 à 1 mm pour les rotifères, et de 0,2 à plus de 2 mm dans le cas des crustacés. La biomasse du zooplancton peut varier naturellement par un facteur 10 à 100 entre les lacs d'une même région (Patalas, 1971; Yan, 1986; Canfield & Jones, 1996). Au sein d'un même lac, elle peut varier du double au quintuple au cours des saisons (Lewis, 1978) et au cours des années (Yan, 1986).

Le zooplancton constitue une part importante mais très variable de la diète de nombreux poissons (Galbraith, 1967; Hutchinson, 1971; Wong & Ward, 1972; Boisclair & Leggett, 1989). Le zooplancton se nourrit à son tour de phytoplancton (Infante & Edmonson, 1985), de bactéries et de détritus. Pour cette raison, le zooplancton s'est vu attribué un double rôle écologique - celui de proie et de prédateur - rôle qui ne cesse aujourd'hui d'alimenter les débats sur les facteurs qui contrôlent la biomasse des communautés aquatiques (Carpenter, Kitchell & Hodgson, 1985; McQueen, Post & Mills, 1986; Persson *et al.,* 1992; Powers, 1992). Selon sa quantité et sa composition, le zooplancton peut également influencer la stratification thermique des lacs (Mazumder *et al.*, 1990), le recyclage des éléments nutritifs (Vadstein *et al.*, 1995) et le rendement en chlorophylla *a* (Mazumder, 1994). Le zooplancton a donc des rapports multiples avec plusieurs caractéristiques importantes des lacs. Vu l'importance des lacs dans le paysage canadien (8% de la surface totale du pays à l'exclusion des Grands Lacs), on peut se demander si les communautés de zooplancton ne sont pas affectées par les coupes forestières et les feux de forêt pourtant si fréquents dans la forêt boréale.

La forêt boréale canadienne et ses facteurs de perturbation

La forêt boréale ceinture $12 \cdot 10^6$ km^2 de l'hémisphère nord, soit 3% des surfaces émergées, ou le quart des surfaces boisées de la planète. Une telle masse végétale joue un rôle important dans le cycle de l'eau et du carbone, tant à l'échelle locale que planétaire. Près de 40% de la forêt boréale se retrouvent en terre canadienne et occupent ainsi environ 35% de la surface totale du pays (Atlas national du Canada, 1996). La forêt boréale montre une composition variable selon que l'on se situe à l'ouest du pays, sur les plaines sédimentaires (dominance par le peuplier faux-tremble) ou à l'est, sur le bouclier précambrien (dominance par l'épinette noire). Elle abrite une variété de communautés animales et végétales, terrestres et aquatiques. Elle assure l'emploi de plus de 15% de la main-d'oeuvre canadienne dans les secteurs de l'industrie forestière, minière, hydro-électrique et, dans une moindre mesure, agricole, piscicole et touristique. Bien que l'on puisse faire remonter l'existence de la forêt boréale à 15 millions d'années, celle en place aujourd'hui en Amérique du Nord s'est développée entre 12 500 et 6 000 ans, suite à la plus récente période glaciaire (Gagnon, 1995). Depuis toujours, les feux ont participé à l'évolution du paysage boréal avec des cycles de 100 à 500 ans selon qu'il s'agisse d'un climat continental ou maritime (Gagnon, 1995). L'existence d'espèces d'arbres dont les graines ne peuvent se développer qu'après le passage d'un feu, tel le pin gris (*Pinus* *divaricata*), témoigne de l'étroite relation entre la forêt boréale et le feu (Bergeron & Charron, 1995). On considère aujourd'hui que les feux sont essentiels au maintien de la productivité de la forêt boréale (Messier, 1995).

Comparée aux millions d'années pendant lesquelles le feu a contribué à modeler le paysage de la forêt boréale, les quelques décennies qui ont vu se développer l'industrie forestière et ses coupes paraissent insignifiantes. Pourtant, en l'espace d'un siècle, les surfaces de forêt déboisées annuellement par l'industrie forestière au Canada ont atteint près de 10 000 km^2, soit une surface comparable à celle des feux de forêt (Figure 1). Les effets de la coupe forestière ont fait l'objet d'études portant surtout sur les caractéristiques chimiques des ruisseaux. Ainsi, il est généralement admis que l'été suivant une coupe à blanc, il peut y avoir, dans les ruisseaux, une augmentation de la température de l'eau (Holtby, 1988), un accroissement de la biomasse des saumons (Bilby & Bisson, 1992), une augmentation des concentrations de matières en suspension (Webster *et al.,* 1990), de potassium, de phosphore, d'azote, de nitrate et de chlorophylle *a* (Jewett *et al.,* 1995; Likens *et al.,* 1970; Nicolson, 1975), ainsi qu'une augmentation de la densité d'organismes benthiques (Murphy, Hawkins & Anderson, 1981). Seules la concentration de sulphate (Likens *et al.,* 1970) et la diversité des macroinvertébrés (Newbold, Erman & Roby, 1980; Reynolds *et al.,* 1994) semblent diminuer. Les effets des coupes sur les systèmes lacustres ne sont pas aussi bien étudiés, mais pourraient inclure des augmentations dans la concentration de phosphore et dans la productivité primaire (Rask, Arvola & Salonen, 1993; Rask *et al.,* 1998), ainsi qu'une diminution de la biomasse de l'omble de fontaine (Bérubé & Lévesque, 1998). Par opposition aux coupes forestières, les effets des feux de forêt sont moins bien étudiés en raison de leur caractère imprévisible. Certains auteurs ont cependant noté une augmentation des concentrations de phosphore, d'azote, de potassium (Schindler *et al.*, 1980; Bayley *et al.,* 1992), des matières en suspension (Beaty, 1994) et un changement dans la composition du benthos (Minshall, Robinson & Lawrence, 1997).

La coupe forestière assimilée à une perturbation naturelle

Les feux de forêt et les épidémies d'insectes ont de tout temps ravagé d'importantes étendues de la forêt boréale. Que la forêt boréale soit capable de se maintenir en dépit de telles perturbations naturelles a fait germer l'idée selon laquelle les coupes forestières industrielles seraient assimilables aux feux de forêt. Autrement dit, si la forêt, sa flore et sa faune sont adaptées à la présence de feux de forêt, pourquoi ne le seraient-elles pas également aux coupes forestières? (La nature n'y verrait que du feu...) En reproduisant certaines des caractéristiques des feux, notamment la perte de couvert forestier sur plusieurs dizaines d'hectares, la coupe à blanc peut être considérée, selon certains, comme un outil d'aménagement qui participe au maintien de la productivité de la forêt boréale, de concert avec les feux de forêt (Messier, 1995). Toutefois, les effets respectifs de la coupe et des feux sur les écosystèmes aquatiques demeurent à ce jour peu connus.

Les bio-indicateurs

Une des questions centrales en écologie est de savoir comment les communautés répondent aux perturbations, qu'elles soient naturelles (cyclones, éruptions volcaniques, innondations, feux de forêt etc.) ou d'origine anthropique (radiations, pluies acides, contamination par les pesticides, coupes forestières etc.). À ce sujet, les idées de Odum (1969; 1985) ont inspiré plusieurs travaux. Selon lui, toute perturbation environnementale serait accompagnée d'une inhibition, voire d'une régression du phénomène de succession qui marque le développement «normal» de tout écosystème, à savoir le passage de communautés d'organismes peu abondants, peu diversifiés, de petite taille et très productifs, à des communautés d'organismes abondants, très diversifiés, de grande taille et peu productifs. Cette hypothèse a été vérifiée dans certains cas: les radiations peuvent entraîner une diminution dans la taille des communautés forestières (Woodwell, 1970); les pluies acides sont généralement accompagnées d'une diminution dans la richesse des communautés zooplanctoniques (Minns *et al.*, 1990; Locke, 1992); la contamination par les pesticides entraîne une réduction dans la taille des communautés zooplanctoniques (Havens & Hanazato, 1993), tout comme la pollution thermique (Moore & Folt, 1993) et les activités récréatives humaines (Harig & Bain, 1998). Plusieurs de ces études portent sur le zooplancton car, en plus de jouer un rôle-clé dans le fonctionnement des écosystèmes lacustres, il est facile à échantillonner, contrairement aux poissons, et conserve des caractéristiques propres au monde animal (recherche et ingestion de nourriture, évitement des prédateurs), contrairement au phytoplancton. À notre connaissance, il n'existe à ce jour aucune étude sur les effets comparés des coupes et des feux sur les communautés zooplanctoniques.

La recherche d'un signe indiquant une atteinte à l'intégrité d'un écosystème pose un problème de taille clairement énoncé par Schindler (1987: 11): à quel moment une caractéristique-clef de l'environnement commence-t-elle à varier au-delà de l'étendue normale, «naturelle» de variation? Le défi posé est double. D'abord, il nous faut disposer d'un système «naturel», c'est à dire un système qui soit encore vierge de toute perturbation environnementale. Une telle tâche s'avère de plus en plus difficile étant donné la dispersion sans cesse accrue de perturbations environnementales d'origine anthropique à toutes les échelles, sans tenir compte de l'omniprésence de perturbations naturelles de toutes sortes. Une fois un tel système ciblé, il nous faut en définir la variabilité intrinsèque de façon à ce qu'il puisse servir de point de référence pour d'autres systèmes que nous croyons altérés suite à diverses perturbations. Nous avons vu précédemment que la biomasse du zooplancton (par unité de volume) pouvait varier naturellement par un facteur de dix ou plus entre les lacs d'une même région. Mais qu'en est-il de la richesse spécifique, de la composition en espèce et de la structure en taille? Tant que nous ne connaîtrons pas la variabilité naturelle des diverses caractéristiques d'un système, il nous sera difficile de poser un diagnostic quant à l'état de santé d'un système perturbé. Vu la difficulté logistique de travailler à l'échelle des écosystèmes (plusieurs centaines de kilomètres carrés, plusieurs années), on comprend mieux l'état embryonnaire de nos connaissances sur les effets des perturbations environnementales.

Le Réseau de centres d'excellence en Gestion durable de la forêt

L'importance de l'industrie forestière au Canada, tant par sa contribution à l'économie du pays que par les questions qu'elle soulève quant à ses effets sur l'écosystème, a contribué à la création, en 1995, du Réseau de centres d'excellence en Gestion durable de la forêt. Regroupement de ressources humaines, matérielles et financières des secteurs gouvernemental, industriel et académique, le Réseau a, entre autres mandats, celui d'étudier les fondements écologiques de la gestion durable des forêts (Réseau de centres d'excellence sur la gestion durable des forêts, 1997). Un des projets de recherche menés sous ce volet vise à comparer les effets des coupes à blanc et des feux de forêts sur les lacs de la Haute-Mauricie dans la province de Québec (Carignan, D'Arcy & Lamontagne, 2000).

Le plan expérimental

Trente-huit lacs de la Haute-Mauricie (Figure 2) ont été échantillonnés trois fois par année et ce, depuis 1996. Ces lacs forment trois groupes caractérisés par différentes conditions de bassin versant: déboisé par la coupe à blanc en 1995 (neuf lacs), brûlé par les feux de forêt en 1995 (neuf lacs), ou intacts (20 lacs). En plus du zooplancton, dont cette thèse fait état, le phytoplancton, le poisson et la qualité chimique de l'eau ont fait l'objet d'échantillonnages et d'analyses par d'autres groupes de recherche (Carignan, D'Arcy & Lamontagne, 2000; Planas *et al.*, 2000; St-Onge & Magnan, 2000).

Cette étude consiste donc à comparer une série de lacs aux bassins versants intacts à une série de lacs dont les bassins versants ont été coupés ou brûlés. Comme le facteur à l'étude est la condition du bassin versant (intact, coupé ou brûlé), la sélection des lacs s'est faite de façon à minimiser les autres facteurs de variation qui pourraient s'ajouter aux effets des coupes et des feux, notamment ceux relatifs à la morphométrie des lacs et des bassins versants. En effet, la morphométrie est un facteur dont il importe de minimiser la variation puisqu'elle peut influencer la chimie de l'eau (Schindler, 1971; Rasmussen, Godbout & Schallenberg, 1989) ainsi que les communautés planctoniques (Patalas, 1971; Duarte & Kalff, 1989). Comme les lacs des trois groupes viennent de la même région géographique, géologique, climatique et qu'ils sont semblables en terme de profondeur, de superficie et de surface de bassin versant (Carignan, D'Arcy & Lamontagne, 2000), nous avons de bonnes raisons de croire que les lacs échantillonnés dans le groupe de référence sont représentatifs – au point de vue chimique et biologique – des lacs inclus dans les groupes «coupés» ou «brûlés». Une analyse de redondance de trois caractéristiques fondamentales de la morphométrie des lacs et des bassins versants (aire du lac, rapport de drainage, profondeur maximale) en fonction de la condition du bassin versant vient appuyer les résultats des analyses de variance présentées à ce sujet dans Carignan et al. (2000) (Figure 3).

Biomasse, assemblages d'espèces et structure en taille des communautés zooplanctoniques

Dans cette thèse, nous examinons trois attributs fondamentalement différents de la structure des communautés zooplanctoniques: la biomasse (masse de zooplancton par volume d'eau), les assemblages d'espèces et la structure en taille. Le suivi des variations de biomasse se présente comme le plus simple des indices diagnostics de l'état de santé d'une communauté (Schaeffer, Herricks & Kerster, 1988). Nous postulons dans le premier chapitre que la biomasse du zooplancton devrait être plus élevée dans les lacs perturbés (bassins versant déboisés par la coupe ou par les feux) que dans les lacs de référence. Comme mentionné précédemment, le déboisement d'un bassin versant entraîne généralement un lessivage des éléments nutritifs du sol vers les plans d'eau. Un apport accru en éléments nutritifs devrait stimuler, dans un premier temps, la croissance des producteurs primaires (notamment le phytoplancton) et, par lien interposé, la biomasse des producteurs secondaires, en l'occurrence le zooplancton. Les résultats de ce premier chapitre présentent une avancée des connaissances sur les effets des perturbations de bassins versant sur le zooplancton notamment parce nous comparons simultanément les effets des coupes à ceux des feux, et parce que nous en suivons les effets immédiats (une année après coupe) et à moyen terme (deux et trois années après coupe). L'étude se démarque également de nombreuses autres études ayant cherché à relier la biomasse du zooplancton à divers facteurs environnementaux et ce, en établissant la puissance des tests statistiques utilisés pour les tests d'hypothèses. Ces aspects sont rarement considérés dans les travaux d'écologie portant sur les relations entre biomasse et facteurs environnementaux.

La biomasse totale du zooplancton représente en fait une sommation des biomasses des espèces qui composent la communauté. Deux lacs peuvent supporter des biomasses de zooplancton équivalentes mais néanmoins montrer des communautés très différentes en termes d'espèces présentes (Hellawell, 1986). Il existe en général une étroite relation entre les espèces de zooplancton qui peuplent un lac et les caractéristiques physiques, chimiques et biotiques de ce dernier. Selon le concept de niche développé par Hutchinson (1957, cité dans Begon *et al.* 1986: 73), chaque espèce présente une tolérance caractéristique à un ensemble de facteurs environnementaux. La présence d'une espèce dans un milieu donné serait donc conditionnelle à la réunion de plusieurs conditions environnementales. Une altération des conditions environnementales peut ainsi entraîner une variation dans l'abondance d'une, ou plusieurs espèces. De telles variations dans les patrons d'abondance de plusieurs espèces de zooplancton (ou «assemblages d'espèces») ont déjà été reliées à diverses perturbations anthropiques telles l'eutrophisation (Attayde & Bozelli, 1998), l'acidification (MacIsaac, Hutchinson & Keller, 1987; Pinel-Alloul *et al.*, 1990), ou le degré de développement résidentiel du rivage (Stemberger & Lazorchak, 1994). Aucune étude à ce jour n'a examiné si les assemblages d'espèces de zooplancton varient en fonction des perturbations par la coupe forestière et les feux de forêt. Dans le deuxième chapitre, nous répondons à cette question. Nous y examinons également une autre caractéristique importante des communautés, à savoir la richesse spécifique (le nombre d'espèces identifiées par lac). Selon la *Intermediate Disturbance Theory* (Connell, 1978; Huston 1979), la richesse d'une communanté est optimale à des niveaux intermédiaires d'intensité et de fréquence de perturbations. Bien que cette théorie ait pu être vérifiée dans certains cas (e.g. Sommer, 1995), elle suppose une étendue d'intensité de perturbation qu'il est impossible de connaître a priori. Par ailleurs, le modèle de rétrogression de Odum (1969, 1985) que nous avons mentionné précédemment, suggère que les perturbations devraient freiner, voire renverser, le processus naturel de succession autogénique et ainsi entraîner une diminution de la richesse des communautés. De fait, des diminutions de la richesse des communautés zooplanctoniques ont été documentés dans le cas de l'acidification (Minns *et al.*, 1990), l'eutrophisation (Schindler, 1990) et la contamination par les métaux (Havens, 1994). Par ailleurs, les perturbations environnementales peuvent parfois entraîner une complexification de l'habitat et, du même coup, augmenter la richesse des communautés qui y vivent (Rapport, Riegier & Hutchinson, 1985). Les relations entre richesse et environnement paraissent donc complexes et encore mal connues. Aucune étude à ce jour n'a examiné les effets de la coupe et des feux sur la richesse des communautés zooplanctoniques.

Dans le troisième chapitre, nous abordons la structure en taille des communautés zooplanctoniques. L'analyse de la structure en taille d'une communauté fait abstraction des espèces qui la composent pour ne se concentrer que sur la biomasse relative des différentes classses de taille d'organismes. Une seule et même classe de taille peut ainsi inclure différentes espèces. L'intérêt d'une telle approche réside dans le fait que de nombreux processus phyiologiques varient en fonction de la taille des organismes (Peters, 1983). Par exemple, les petits organismes ont généralement des taux de croissance spécifiques plus élevés que les organismes plus grands. Ces petits organismes auraient donc l'avantage sur les organismes plus grands lorsqu'il s'agit de coloniser un espace nouvellement créé suite, par exemple, à une perturbation environnementale. De fait, plusieurs études ont montré une tendance à la diminution de la taille des organismes zooplanctoniques dans les milieux perturbés par l'eutrophisation (Sprules & Munawar, 1986), les activités récréatives humaines (Harig & Bain, 1998), l'acidification (Schindler, 1990) et la contamination chimique (Havens & Hanazato, 1993). Le chapitre III examine si cette tendance à la diminution de taille des communautés zooplanctoniques s'observe également dans le cas de perturbations par les coupes et les feux.

La coupe forestière et les feux de forêt sont des phénomènes courants qui transforment le paysage de la forêt boréale. L'habitat des communautés aquatiques s'en voit modifié mais on ne sait pas si ces modifications sont suffisamment marquées pour entraîner un changement dans les communautés mêmes. Cette thèse examine trois aspects fondamentalement différents des communautés zooplanctoniques: la biomasse, la composition en espèces et la structure en taille. Elle ne prétend pas pouvoir élucider les mécanismes par lesquels les coupes ou les feux entraînent des changements dans ces attributs des communautés zooplanctoniques. L'élucidation des mécanismes suppose d'abord que l'on sache, en premier lieu, si les coupes et les feux entraînent bel et bien des changements au niveau de la structure des communautés zooplanctoniques. C'est ce que fait cette thèse. Le zooplancton ne représente bien sûr qu'une seule communauté aquatique parmi bien d'autres qui peuvent être affectées par les pertrubations de bassins versants. Mais les liens qui relient le zooplancton aux producteurs primaires, aux poissons et à la qualité de l'eau sont multiples. Il importe donc de savoir si les coupes et les feux entraînent des changement dans la structure des communautés zooplanctoniques des lacs de la forêt boréale canadienne.

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Figure 1. Importance relative des coupes forestières, des feux de forêt, et des insectes ravageurs dans les pertes de surfaces boisées au Canada. Pertes annuelles en km^2 (moyennes des années 1981 à 1995) (Service canadien des forêts, 1998).

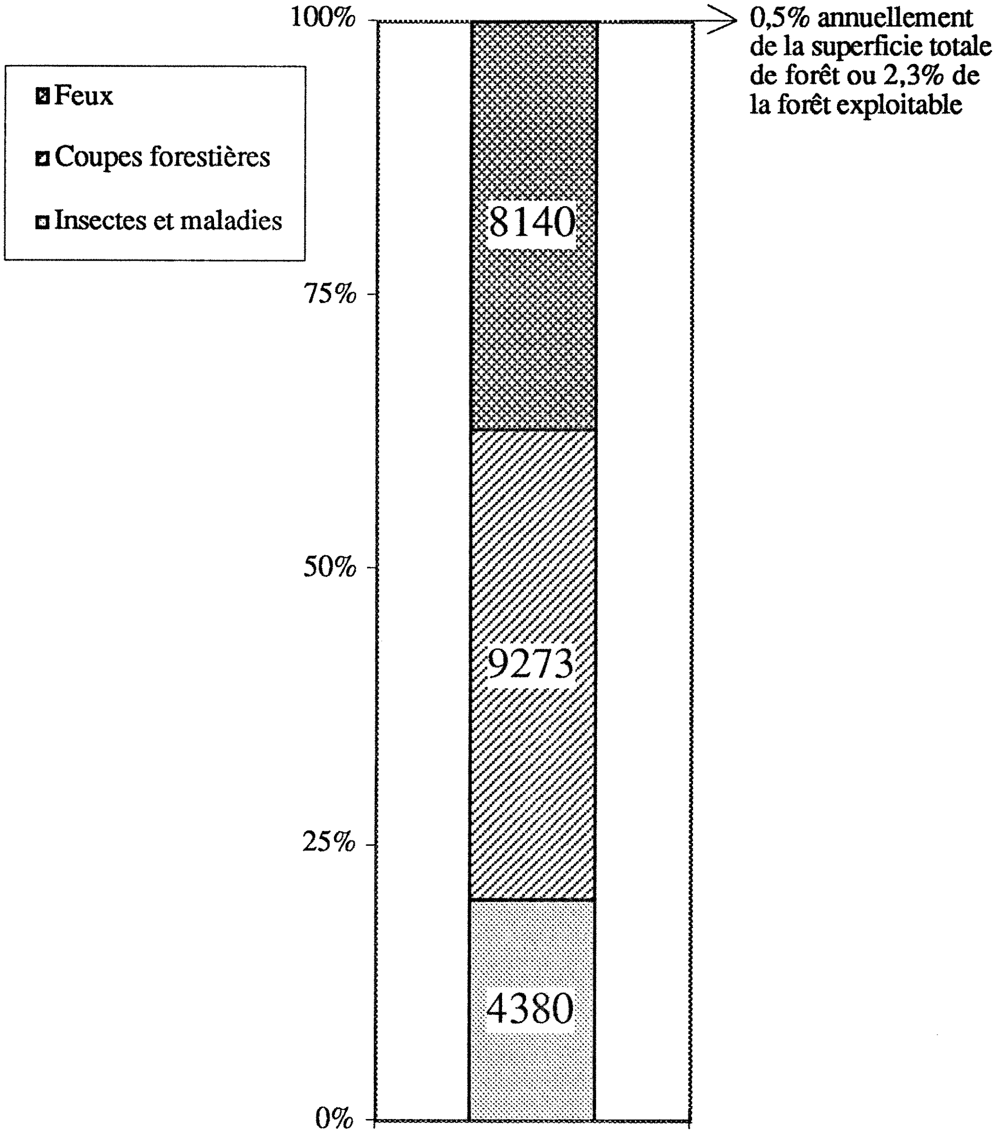
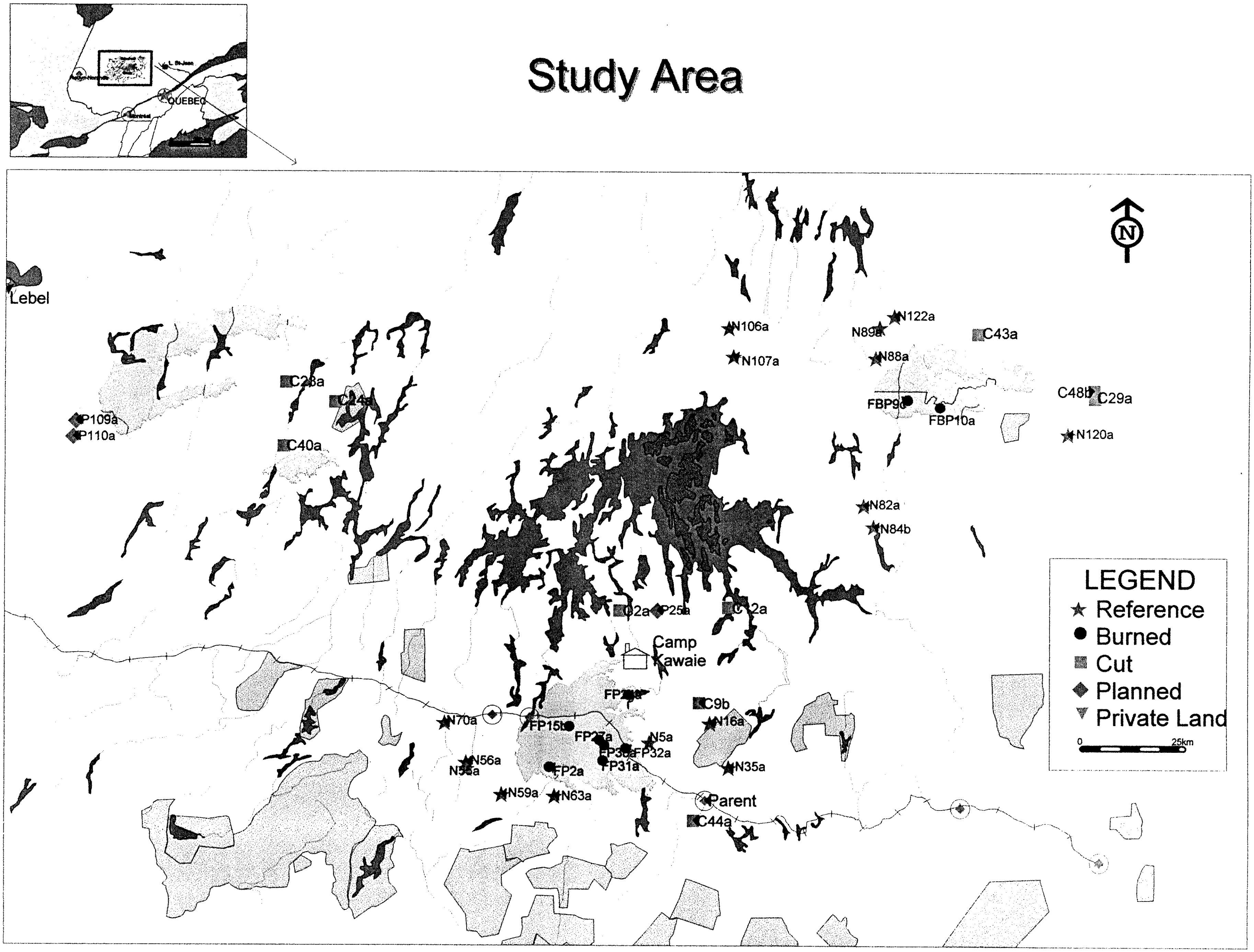


Figure 2. Carte de la région à l'étude.

Study Area


QUEBEC
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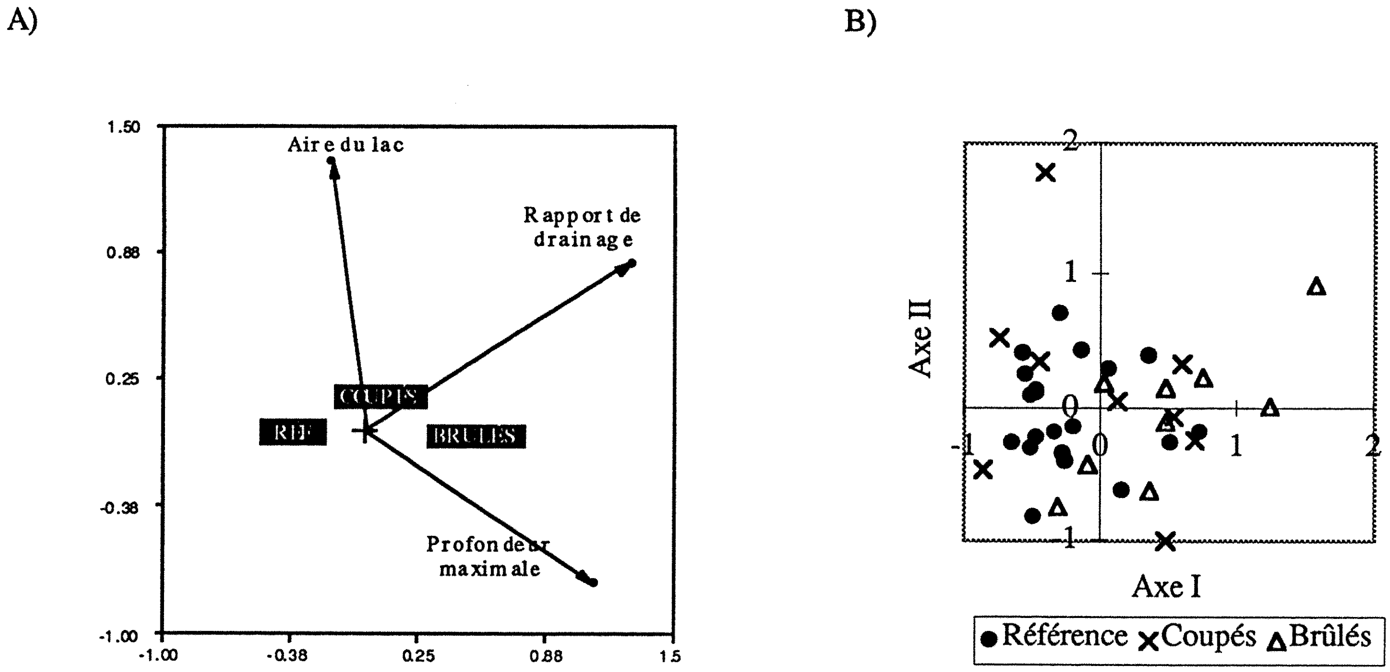
N122a
N89a
N88a
C43a
C48b
C29a
FBP9a
FBP10a
N120a
C28a
C24a
C40a
P109a
P110a
N82a
N84b
C2a
P25a
C12a
Camp Kawaie
FP28a
C9b
N16a
N70a
FP15b
FP27a
N5a
FP30a
FP32a
N56a
N55a
FP2a
FP31a
N35a
N59a
N63a
Parent
C44a
LEGEND
★ Reference
● Burned
■ Cut
◆ Planned
▼ Private Land
0
25km

Figure 3. Analyse de redondance de trois caractéristiques morphométriques fondamentales des bassins versants et de leurs lacs en fonction des trois groupes de lacs à l'étude: référence (n=20), aux bassins versants déboisés par la coupe (n=9) ou par les feux (n=9). A) Diagramme en double projection des centroïdes des trois groupes de lacs et des vecteurs-descripteurs. B) Diagramme d'ordination des 38 lacs. L'appartenance à l'un ou l'autre groupe n'explique qu'une fraction (8,9%) non significative (P=0,11, 999 permutations) de la variabilité dans l'aire du lac, la profondeur maximale et le rapport de drainage.



CHAPITRE I – Do logging and forest fires influence zooplankton biomass in Canadian Boreal Shield lakes?

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Abstract

Zooplankton biomass was assessed in 20 reference lakes, 9 logged- and 9 burned-watershed lakes during three summers following watershed disturbances by logging or wildfires. Biomass of cladocerans, calanoids, cyclopoids and rotifers was quantified in the 38 lakes for the first year following disturbances. Limnoplankton biomass in four size fractions was quantified during three years following disturbances. One year after disturbances, burned-watershed lakes supported on average 59% more biomass of the rotifer size fraction of limnoplankton (100-200 μm) than reference lakes, while logged-watershed lakes supported 43% less calanoid biomass. Two years after disturbances, differences in limnoplankton biomass between burned-watershed lakes and reference lakes were more pronounced than during the first year, while logged-watershed lakes supported levels of limnoplankton biomass no different than reference lakes. Three years after disturbances, no significant variations could be detected among the three groups of lakes for any of the limnoplankton size fractions. The proportion of watershed area impacted by logging activities was on average less than half the proportion impacted by wildfires. Nonetheless, both types of disturbances seemed to have opposite effects on the zooplankton biomass during the first year, and the effects did not extend beyond two years

Résumé

La biomasse du zooplancton a été mesurée dans 20 lacs aux bassins versants intacts, neuf lacs aux bassins versants déboisés par la coupe forestière (lacs C) et neuf lacs aux bassins versants brûlés par des feux de forêt naturels (lacs F), et ce, pendant les trois étés qui ont suivi les perturbations de bassins versants. Pendant la première année après perturbations, la biomasse de limnoplancton comprise entre 100 et 200 μm, composée principalement de rotifères, était en moyenne 59% plus élevée dans les lacs F que dans les lacs de référence, tandis que la biomasse des calanoïdes était 43% plus faible dans les lacs C. Pendant la deuxième année, les différences de biomasse de limnoplancton entre lacs F

et lacs de référence étaient encore plus élevées comparées à la première année, tandis que les lacs C montraient des biomasses équivalentes à celles des lacs de référence. Pendant la troisième année, aucune différence de biomasse n'était détectable entre les trois groupes de lacs. Les effets des feux de forêt sur la biomasse du zooplancton semblent opposés à ceux des coupes forestières pendant la première année et ne se prolongent pas au-delà de la deuxième année.

Introduction

Wildfires and logging each remove about 10,000 km^2 of Canada's 4.5 million km^2 forest each year (Forestry Canada 1991). New strategies in forest management are based on the assumption that emulating natural disturbances such as wildfires in logging practices will sustain boreal forest dynamics and biodiversity (Hunter 1993). Such strategies, however, were developed without considering aquatic ecosystems, even though water represents 8% of Canada's surface area. Comparing the impacts of wildfires and logging on lake water quality and biota is a necessary step towards developing forest management practices which take into account the global impacts of logging on the forest-lake ecosystem.

Stream concentrations of particulate organic matter, phosphorus, nitrogen and ions can increase following forest fires (Bayley et al. 1992) and clear-cutting (Likens et al. 1970). Following watershed disturbance, the biomass of stream macro-invertebrate communities has been shown to increase in some cases (Burton and Ulrich 1994) but not in others (Minshall et al. 1997). In comparison to the number of studies on streams, little work has addressed the consequences of watershed disturbance on lake aquatic communities. In some cases, forest harvesting was associated with increases in chlorophyll *a* (chl-a) concentrations and primary production (Rask et al. 1993), moderate increases in cladoceran and copepod density (Rask et al. 1998), and decreases in catch and biomass per unit effort of brook trout (Bérubé and Lévesque 1995). In other cases, differences between logged-watershed lakes and reference lakes in chl-a, total phosphorus (TP), total nitrogen (TN) and dissolved organic carbon concentrations (DOC) were undetectable (Lehmann 1994). Presently, confounding factors such as the type of disturbance (logging or fire), the time elapsed since the disturbance and the extent of natural variability render any statement on the differential impacts of logging and fires on lake biota questionable.

Zooplankton represent an essential component of lake biota: by grazing on the phytoplankton community, zooplankton can control algal biomass and size structure (Christoffersen et al. 1993), contribute to nutrient recycling (Lehman 1980), increase water transparency (Lampert et al. 1986), and increase mixing depth (Mazumder et al. 1990). Zooplankton biomass in Canadian Boreal Shield lakes is positively related to the concentration of TP and TN (Yan 1986). It is therefore likely, but yet unknown, that zooplankton biomass in logged- and burned-watershed lakes is somewhat higher than in undisturbed-watershed lakes.

The present study is the first to compare the effects of forest fires and logging on the biomass of zooplankton in Canadian Boreal Shield lakes. We present the results of three years of zooplankton sampling in 38 lakes of central Québec characterised by different watershed conditions: undisturbed, logged and burned. We predict that zooplankton biomass (mass per unit volume of water) will be higher in logged- and burned-watershed lakes than in undisturbed-watershed lakes.

Materials and methods

STUDY LAKES AND SAMPLING DESIGN

The study was conducted in 38 boreal lakes located on the Canadian Shield in Québec, around the Gouin reservoir. Lakes were distributed in three groups representing different watershed conditions: undisturbed (20 reference lakes), logged (9 lakes) and burned (9 lakes). The logging and natural forest fires all occurred in 1995, about one year before the beginning of the study. Logged-watershed lakes had 7% to 73% of their watershed area clear-cut in 1995, and had 20 m buffer zones of unharvested vegetation surrounding the lakes. Burned-watershed lakes had 50% to 100% of their watershed burned by natural forest fires, also in 1995. Lakes were chosen on the basis of comparable lake and watershed morphometry among the three groups of lakes (Table 1). Details on bedrock geology, landscape features, climate and vegetation are presented in Carignan et al. (2000). The lakes were sampled three times per year, in May-June, July and September of 1996, 1997 and 1998. All were sampled within five days, between 6:00 and 15:00.

ZOOPLANKTON SAMPLING AND BIOMASS DETERMINATION

Zooplankton were sampled at the deepest point of the lakes with a 53 µm mesh cantilevering net (Filion et al. 1993) from 1 m above the sediment to the surface. Filtered water volume varied between 80 and 1200 L depending on lake depth. Zooplankton were narcotised in the field with carbonated water and preserved in 4% formaldehyde. In the laboratory, the samples were split into four equal fractions with a Folsom splitter; one quarter was used for taxonomic analysis (see details below), one was used for size fractionation and organic mass determination of limnoplankton (see details below). The two residual quarters were kept for later studies and reference material.

Taxonomic analyses were performed on 10 mL sub-samples of the 1996 samples. Zooplankton were identified to species, by following the keys of Edmondson (1959), Brandlova et al. (1972) and Smith and Fernando (1978). Naupliar and copepodite stages of calanoids were distinguished from those of cyclopoids. To estimate specific biomass, we measured the size of the first 30 specimens of each crustacean (length) and rotifer (length and width) species. Mean size values were converted to dry biomass using the length-mass relationships developed by Malley et al. (1989). Specific dry mass values were summed to obtain the biomass of four taxonomic groups (cladocerans, calanoids, cyclopoids and rotifers) and total zooplankton biomass. Zooplankton biomass was expressed in mg dry mass per cubic metre.

Size-fractionated limnoplankton measurements were performed on the 1996, 1997 and 1998 samples. Each sample was sieved through a sequential array of nets of decreasing mesh sizes: 500, 200, 100 and 50 µm in order to obtain four size fractions: 50-100 µm, 100-200 µm, 200-500 µm and > 500 µm. The material collected on each net was then back-washed and filtered onto pre-combusted GF/A (Whatman) glass fiber filters, dried at 40°C for 18 hours, weighed, ashed at 500°C for 18 hours and weighed again. Limnoplankton organic mass for each size fraction was calculated as the difference between the two mass measurements and expressed in mg of ash-free dry mass (AFDM) per cubic meter.

Species composition of limnoplankton size fractions was determined under 20 X magnification prior to drying. The > 500 µm size fraction was principally composed of *Holopedium gibberum* (47% on average of the dry mass of this size fraction), *Daphnia* spp. (21%), adult calanoids (16%) and adult cyclopoids (15%). Hence, in this paper, the > 500 µm size fraction will be referred to as the crustacean size fraction. The 200-500 µm size fraction was generally composed of calanoid copepodites (43%), cyclopoid copepodites (32%), nauplii (12%) and bosminids (6%); it will be referred to as the copepodite size fraction. The 100-200 µm size fraction was mostly composed of nauplii, rotifers and algae while the 50-100 µm consisted of rotifers and algae. These will be referred to as the rotifer and algal size fractions, respectively.

Statistical analyses

To test if watershed condition was a significant source of variation in zooplankton or limnoplankton biomass for the entire ice-free season, one-way repeated measures analyses of variance were performed for each zooplankton variable (Sokal and Rohlf 1981: 284). The three samplings performed in each lake (June, July, September) were treated as repeated measures. In the case of limnoplankton, a separate repeated measures analysis of variance was performed for each of the three years following watershed disturbance (1996, 1997, 1998). Homoscedasticity was tested with the Bartlett test (Sokal and Rohlf 1981: 403).

Where F tests revealed a significant treatment effect (α=5%), the Scheffe multiple range test was performed to assess where differences lay (SAS Institute Inc. 1988). Where F values were declared non significant, a power analysis was performed to quantify the risk of type II error (Cohen 1988). Analyses of variance were also performed for each sampling period separately to determine when among-group differences in biomass were strongest.

To examine if zooplankton biomass was related to disturbance intensity (percent of watershed area logged or burned) independently of disturbance type (logging or fire), regression analyses were performed between the different variables of zooplankton biomass (dependent variables) and the arc sine transformation of disturbance intensity (independent variable). Ordinary least-square regression was used because the measurement error on disturbance intensity was likely smaller than that on zooplankton biomass.

Four lakes in the reference group in 1996 were eliminated from the limnoplankton biomass analyses for the years 1997 and 1998 because these lakes had their watershed logged during the fall of 1996 or winter 1997. In addition, two reference lakes were not sampled in May 1998. As a result, the sample size for the reference group was 38 in 1996, 34 in 1997 and 32 in 1998 (except for July and September 1998: n=34). All analyses were performed on log-transformed values of zooplankton and limnoplankton biomass.

Results

AMONG-GROUP DIFFERENCES IN ZOOPLANKTON BIOMASS, 1996

There was no detectable difference in the biomass of total zooplankton, cladocerans, and cyclopoids among the three groups of lakes (P>0.25), although burned-watershed lakes had consistently higher biomass than reference lakes (Fig. 1). Calanoid biomass was 43% lower in logged-watershed lakes than in reference lakes (p=0.01, Fig. 1). Among-group variation in rotifer biomass was not significant (p=0.09), although burned-watershed lakes supported 74% more rotifer biomass than reference or logged-watershed lakes (Fig. 1).

AMONG-GROUP DIFFERENCES IN LIMNOPLANKTON BIOMASS, 1996 TO 1998

During the first year following watershed disturbances (1996), the biomass of the rotifer size fraction of limnoplankton was on average 59% higher in burned-watershed lakes than in reference lakes (*p*=0.03, Fig. 2D). There were no significant variations in the other size fractions among groups of lakes one year after disturbances, although some lakes among the burned group tended to support greater biomass of limnoplankton than reference lakes, especially for the crustacean size fraction (+41%, Fig. 2B), and the algal size fraction (+23%, Fig. 2E).

This tendency for burned-watershed lakes to support higher limnoplankton biomass than reference lakes was even more pronounced two years following watershed disturbances (Fig. 2): average percent increases ranged from 91% for the rotifer size fraction (*P*=0.02, Fig. 2D) to 65% for the crustacean size fraction (*P*=0.08, Fig. 2B). Increases in the other size fractions of limnoplankton were less than 30% and non-significant (*P*>0.45, Fig. 2). As a result of these increases in each size fractions in 1997, total biomass of limnoplankton was 50% greater in burned-watershed lakes than in the reference lakes (*P*=0.08, Fig. 2A).

The logged group of lakes supported levels of limnoplankton within ±25% of that of the reference group during the three years of the study. Differences were never significant. During the third year following watershed disturbances, limnoplankton biomass levels for all size fractions in the logged and burned groups were within ±25% of that of the reference group of lakes (*P*>0.3).

The observed among group differences in mean biomass levels of total zooplankton and total limnoplankton relative to the reference group were generally within ±50% (Figs 1 and 2A). In contrast, the confidence intervals on the means of each group were large (Figs 1 and 2A). As a result, the null hypothesis of no effect of watershed condition on total zooplankton and total limnoplankton biomass levels was accepted (Table 2). If, however, the observed heterogeneity among groups of lakes did constitute a true effect of watershed condition, the present study design would have a high probability of not detecting it. This is reflected in the high risks of type II error (Table 2). The same can be said for all other zooplankton variables for which the null hypothesis of no effect was accepted (Table 2). Hence, in the cases where the null hypothesis was accepted, we cannot conclude, with great certainty, that watershed condition does not impact on zooplankton biomass. The size of such effect, however, would be smaller than a 50% difference with the reference group of lakes.

Sampling period constituted a source of variation in zooplankton biomass several fold greater than watershed condition (Table 3). We therefore proceeded to analyse among group variations for each of the three sampling periods separately. Significant among-group differences were detected during the June or July sampling periods , but not during the September sampling period (Table 4). Biomass were generally highest in June, and lowest in September. Results of analyses based on each sampling period (Table 4) were consistent with those based on the entire ice-free season (Table 3): among group variations which were significant for the entire ice-free season were also significant for individual sampling periods. In only one case did analyses by month reveal significant among-group variations not detected by the repeated measure analyses: the rotifer size fraction of limnoplankton in July 1998 was 71% higher in burned-watershed lakes than in reference lakes (Table 4).

The biomass of the rotifer size fraction of limnoplankton in logged- and burned-watershed lakes one year after disturbance was positively related to disturbance intensity (Fig. 3). The relationship for both logged- and burned-watershed lakes could be described by a single regression equation. There was, however, practically no overlap in the ranges of disturbance intensity between the logged and burned groups of lakes. Because extrapolating beyond the range of observations for each of the two groups of lakes is untenable, regression analyses were performed for each set of lakes separately (Fig. 3).

For the logged group of lakes, 77% of the variation in the biomass of the rotifer size fraction could be explained by disturbance intensity (P=0.002). Similar relationships were observed for the algal size fraction (r^2=71%, P=0.004), the copepodite size fraction (r^2=60%, P=0.01), and total limnoplankton (r^2=62%, P=0.01), but not for the crustacean size fraction of limnoplankton nor for any of the taxonomic groups of zooplankton. The regression coefficient for the burned group of lakes was not significant (P=0.57).

Discussion

Our hypothesis of greater zooplankton biomass in disturbed-watershed lakes was supported in the case of burned-watershed-lakes, but not in the case of logged-watershed lakes. These biomass increases in burned-watershed lakes relative to reference lakes are consistent with the greater TP, TN and chl-a concentrations observed in the burned group of lakes (Table 1) and the positive relationships reported between zooplankton biomass and TP and TN (Yan 1986) and chl-a (Pace 1986) in North-American lakes. Greater biomass in burned-watershed lakes was most pronounced for the rotifer size fraction of limnoplankton. Rotifers and, more generally, the smaller components of plankton are known to relate more closely to nutrient or chl-a concentrations than the larger components of plankton in Eastern Canadian oligo-mesotrophic lakes (Currie et al. 1999). It is interesting to note that, although limnoplankton size fractions are composed of many different organisms (cf. Material and methods), there was good agreement between the results of among group differences in the rotifer size fraction of limnoplankton (Fig. 2D) and the rotifer taxonomic group (Fig. 1), one year following disturbances.

While the biomass of the smaller rotifer size fraction of zooplankton was higher in burned-watershed lakes during the first and second years following disturbance, the biomass of the larger crustacean size fraction was higher only during the second year. This could reflect the shorter generation time of rotifers relative to crustaceans (Allan and Goulden 1980), allowing rotifers to exploit the available resources before the crustaceans.

Crustaceans, in contrast, can demonstrate time lags in response to increases in nutrient concentrations (Smith 1969). Alternatively, the greater biomass of the crustacean size fraction in burned-watershed lakes relative to reference lakes observed during the second year could be the result of a lower predation pressure in the burned group of lakes (Brooks and Dodson 1965). There was some indication that the relative density of small yellow perch (< 74 mm), and small lake whitefish (< 119 mm) was reduced in logged and burned-watershed lakes (Magnan and St-Onge 1999), supporting the idea of decreased predation pressure on zooplankton in burned-watershed lakes. Planktivorous fish, however, included more than 10 different species, the total density of which showed no differences among the three groups of lakes (Table 1). The relative importance of nutrient concentration and fish density in relation to zooplankton biomass remains unclear. With respect to the greater biomass of the rotifer size fraction observed in burned-watershed lakes relative to reference lakes during the first and second year after disturbance, it could, hypothetically, result in a decrease in the efficiency of carbon transfer from algae to fish (Stockner and Shortreed 1989). These authors have argued that rotifers can constitute an energy sink by adding to the number of trophic levels through which matter must flow before reaching fish. The importance of such a phenomenon remains to be quantified.

Contrary to our expectations, there was a general tendency, calanoids excepted, for logged-watershed lakes to support zooplankton biomass equivalent to, or slightly lower than, those of reference lakes. This may in part reflect the lower disturbance intensity in logged- than in burned-watershed lakes (Table 1). Forestry practices removed on average 38% of forest cover in the logged group while natural forest fires removed more than 90% in eight out of nine cases (Table 1). In addition, Québec provincial legislations require that a 20 m buffer strip zone of unharvested vegetation be left along lakes and streams. The lower degree of disturbance in logged-watershed lakes compared to burned-watershed lakes, and the buffer strips might have mitigated the nutrient inputs to logged-watershed lakes, thus in part accounting for the absence of detectable zooplankton biomass differences between logged-watershed and reference lakes (with the exception of calanoids). The smaller difference between logged-watershed and reference lakes than between burned-watershed and reference lakes was not only observed for zooplankton biomass, but also for algal biomass and chl-a concentration (Planas et al. 2000), TP, and TN concentrations (Carignan et al. 2000).

Calanoid biomass was clearly lower in logged-watershed lakes than in reference lakes (–43%, P=0.01). Calanoids are often associated with nutrient poor environments (Patalas 1972; Pace 1986). In our study, calanoid biomass across the 38 lakes was negatively correlated with TN (r=–0.40, P=0.01) and chl-a (r=–0.33, P=0.05). This suggests that calanoids did better in the nutrient-poor environments of reference lakes than in the richer logged-watershed lakes. The biomass of cyclopoids, rotifers, and the copepodite size fraction of limnoplankton, however, was also lower in logged-watershed lakes compared to reference lakes, although differences were not significant (Fig. 1 and Fig. 2C). Lower biomass in logged-watershed lakes was also reflected in total zooplankton biomass (Fig. 1) and total limnoplankton biomass (Fig. 2A) one year after logging. Logged-watershed lakes would therefore seem to support lower zooplankton biomass despite higher TP, TN and chl-a concentrations. Dissolved organic carbon (DOC) concentrations in logged-watershed lakes were higher than in reference or burned-watershed lakes (Table 1) and, as a result, light penetration was reduced by 40% compared to reference lakes (Carignan et al. 1999). We suggest that logged watershed-lakes tend to support lower zooplankton biomass than reference lakes despite higher TP and TN concentrations through light limitation of primary productivity.

Among-group differences in the 1998 limnoplankton biomass were weaker than during the first two years following watershed disturbances. The same applies to other environmental variables, for example, the concentrations of nitrate, potassium, sulfate, chloride, and chl-a (Carignan et al. 2000; Planas et al. 2000). Natural regeneration of vegetation on the disturbed watersheds may have contributed to curb phosphorus and nitrogen washout and thereby temper the among-group differences in the biomass of primary producers and zooplankton. Alternatively, nutrient inputs from burned watersheds could have remained high in 1998, with, nonetheless, no appreciable among group differences in limnoplankton biomass. Such a hypothetical scenario could be achieved through increased turn-over rates of primary producers, grazers, and planktivorous fish.

Month to month variability in limnoplankton biomass among groups of lakes may be related to temporal variability in runoff and element load to lakes. Significant among-group differences in limnoplankton biomass usually occurred in the spring and summer periods (June and July sampling periods) rather than during the fall period (September sampling period). The greater response of limnoplankton biomass to watershed disturbances earlier in the year may be related to greater runoff occurring during this period. For the region under study, between 30% and 40% of annual runoff, and presumably element loss from the watershed, occurs during the months of April and May (roughly corresponding to snowmelt). In contrast, less than 14% of annual runoff usually occurs during the months of August and September (S. Lamontagne pers. comm.). Thus, if used as an indicator of watershed disturbance in Shield lakes, limnoplankton should be sampled during the spring and summer periods, when the interactions between the terrestrial and aquatic components of the landscape are greatest.

The present study did not allow us to compare zooplankton biomass between logged- and burned-watershed lakes sharing similar disturbance intensities. The zooplankton biomass differences observed between logged- and burned-watershed lakes can thus be attributed either to a difference in the nature of the disturbance (logging or fire) or, alternatively, to a difference in the intensity of the disturbance, or both. There is good evidence that logging and burning have different effects on the chemistry of water, irrespective of disturbance intensity (Carignan et al. 2000). Whether equivalent zooplankton biomass would have been obtained in logged- and burned-watershed lakes with comparable disturbance intensities is a matter of speculation. The positive relationships observed between the biomass of the algal, rotifer, and copepodite size fractions of limnoplankton and disturbance intensity suggest we could have observed higher biomass in the logged-group of lakes than in reference lakes, had the logging covered a greater proportion of watersheds. High percentages of logged watershed area were seldom achieved, though, in part because the watershed areas were large enough for extensive proportions of them to support unsuitable timber material. Alternatively, it is possible that, with higher percentages of the watershed area logged, the expected increase in plankton biomass would be counteracted by lower light penetration due to increased concentrations of dissolved organic carbon, as already mentioned above.

The biomass values reported in this study were similar to those reported in Yan (1986) for 16 undisturbed Ontario lakes with comparable lake areas and TP concentrations. He presented crustacean biomass values varying from 34 to 103 mg d.w.•m^{-3}, a range comparable to that of 20 to 163 mg d.w.•m^{-3} observed in our set of 20 reference lakes (sum of cladocerans, calanoids and cyclopoids). Although no study has previously reported on the comparative effects of logging and forest fires on zooplankton biomass, Rask et al. (1998) did report on cladoceran and copepod densities in one reference lake and three Finnish lakes with 15% to 33% of the watershed clear-cut. They observed slight increases in the density of cladocerans and copepods in some of the lakes following watershed logging. They did not, however, comment on the magnitude of these increases in comparison to inter-annual, inter-month or inter-lake variability. Their data suggest these sources of variation were hard to separate from that associated with watershed disturbance.

With a sample size of 20 reference lakes, nine logged- and nine burned-watershed lakes, the present study was powerful enough to detect significant among group variations in the following cases: calanoid biomass, one year following disturbances, was 43% lower in logged-watershed lakes than in reference lakes; rotifer size fraction biomass of limnoplankton, one and two years following disturbances, was at least 60% greater in burned-watershed lakes than in reference lakes. The among-group variations in the other taxonomic groups and size fractions were generally smaller than 50% and statistical power was too low to detect potential differences (at α=5%). Because logging activities rarely affect 90% of a watershed's area like wildfires do, and because regulations require that a 20 m buffer strip be left between logged areas and water resources, both types of disturbances could not be compared on the basis of equal disturbance intensities. Nonetheless, as they occur in reality, logging activities and forest fires seem to have opposite impacts on the biomass of zooplankton of Eastern Canadian Boreal Shield lakes. Wildfires seem to be associated with greater zooplankton biomass than reference lakes, especially the smaller, rotifer size fraction of limnoplankton. On the contrary, logging activities seem to be associated with decreases in zooplankton biomass, especially calanoids, in comparison to reference lakes.

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Table 1. Characteristics of the 38 lakes and their watersheds for the three groups of watershed treatment. Means (and ranges) are based on three years of sampling for chemical variables (R. Carignan, pers. comm.). Fish abundances were based on catches in 1996 and 1997 (P. Magnan, pers. comm.).

	Reference ($n = 20$)	Logged ($n = 9$)	Burned ($n = 9$)
Maximum Depth (m)	12 (7-23)	14 (5-30)	17 (10-34)
Lake Area (ha)	44 (14-81)	56 (18-231)	40 (17-64)
Drainage Ratio (Drainage area/Lake area)	5.4 (2.3-15.4)	6.7 (2.0–13.2)	7.1 (2.5–11.6)
Percent Watershed Area Disturbed	0% (0%-1%)	38% (7%-73%)	90% (50%-100%)
pH	6.3 (5.8–7.0)	6.1 (5.7–7.0)	6.3 (5.6–7.2)
Total Phosphorus ($\mu g \cdot L^{-1}$)	6.9 (4.5–11.8)	9.5 (5.4–17.3)	11.8 (5.6–17.3)
Total Nitrogen ($\mu g \cdot L^{-1}$)	213 (118–332)	252 (160–386)	310 (169–747)
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	1.7 (0.8–3.4)	2.0 (1.0–3.3)	3.1 (1.2–5.2)
Planktivores (CPUE)	38 (0.3-206)	26 (8–106)	36 (0.1–128)

Table 2. Power analysis of the *F* tests conducted on zooplankton biomass in three groups of lakes: undisturbed-, logged- and burned-catchments. For each test, the probability associated with type I error is indicated if the null hypothesis of no among group differences was rejected, or the approximate probability of type II error, if the null hypothesis was accepted.

Variable	Year	Null hypothesis	Type I error probability	Type II error probability
Total zooplankton	1996	Accepted		0.75
Cladocerans	1996	Accepted		0.84
Calanoids	1996	Rejected	0.01	
Cyclopoids	1996	Accepted		0.83
Rotifers	1996	Accepted		0.54
Total limnoplankton	1996	Accepted		0.54
	1997	Accepted		0.41
	1998	Accepted		0.92
Crustacean size fraction of limnoplankton	1996	Accepted		0.74
	1997	Accepted		0.56
	1998	Accepted		0.95
Copepodite size fraction of limnoplankton	1996	Accepted		0.64
	1997	Accepted		0.84
	1998	Accepted		0.79
Rotifer size fraction of limnoplankton	1996	Rejected	0.03	
	1997	Rejected	0.02	
	1998	Accepted		0.83
Algal size fraction of limnoplankton	1996	Accepted		0.79
	1997	Accepted		0.92
	1998	Accepted		0.85

Table 3. Relative importance of watershed condition and sampling period as factors accounting for variation in zooplankton and limnoplankton biomass. *F* values and associated probabilities are indicated for each source of variation. Watershed condition was the main effect factor, while sampling period was a nested factor. For the main effect factor, degrees of freedom for the *F* values were 2 in the numerator (v_1) and varied with year in the denominator (v_2=35 in 1996; 31 in 1997; 29 in 1998). For the nested factor, v_1=2, v_2=70 in 1996; 62 in 1997; 58 in 1998.

Variable	Year	*F* value for watershed condition	*p* value for watershed condition	*F* value for sampling period	*P* value for sampling period
Total zooplankton	1996	1.37	0.27	13.8	0.0001
Cladocerans	1996	0.60	0.56	2.7	0.0776
Calanoids	1996	4.83	0.01	6.6	0.0024
Cyclopoids	1996	0.70	0.51	10.3	0.0001
Rotifers	1996	2.58	0.09	35.5	0.0001
Total limnoplankton	1996	2.35	0.11	25.3	0.0001
	1997	2.77	0.08	83.4	0.0001
	1998	0.17	0.85	11.7	0.0001
Crustacean size fraction of limnoplankton	1996	1.27	0.29	11.7	0.0001
	1997	2.69	0.08	53.2	0.0001
	1998	0.06	0.94	7.4	0.0014
Copepodite size fraction of limnoplankton	1996	1.97	0.15	3.9	0.0255
	1997	0.78	0.47	33.0	0.0001
	1998	1.03	0.37	10.3	0.0001
Rotifer size fraction of limnoplankton	1996	4.02	0.03	25.1	0.0001
	1997	4.78	0.02	36.1	0.0001
	1998	0.40	0.68	2.8	0.0708

Variable	Year	*F* value for watershed condition	*p* value for watershed condition	*F* value for sampling period	*P* value for sampling period
Algal size fraction of limnoplankton	1996	0.92	0.41	38.8	0.0001
	1997	0.26	0.78	14.6	0.0001
	1998	0.59	0.56	9.2	0.0003

Table 4. Analysis of variance of zooplankton and limnoplankton biomass by sampling period. Mean biomass values for each watershed treatment type (reference, logged, and burned) were back-calculated from logarithms. Degrees of freedom for the *F* values were 2 in the numerator, and varied with year in the denominator (35 in 1996; 31 in 1997, July and September 1998; 29 in June 1998). Only probabilities (*p*) of less than 0.1 are indicated. When *F* values are significant ($p<0.05$), the results of a Scheffe multiple-comparison of means are indicated by a lower-case letter. Means annotated with a single letter (e.g. "a") are significantly different from other means annotated with a different, single letter (e.g. "b"). Means annotated with multiple letters (e.g. "ab") are not significantly different from either of the named groups.

Variable	Year	Sampling period	Mean zooplankton biomass				
			Reference	Logged-	Burned-	*F*	*P*
Total zooplankton (mg d.w.•m^{-3})	1996	June	59	40	63	1.22	
		July	32	34	37	0.15	
		Sept	23	18	30	1.10	
Cladoceran (mg d.w.•m^{-3})		June	17	15	21	0.15	
		July	10	17	11	0.49	
		Sept	5	8	13	0.94	
Calanoida (mg d.w.•m^{-3})		June	11	6	7	3.02	0.06
		July	8	5	7	1.45	
		Sept	6	3	5	2.73	0.08

Variable	Year	Sampling period	Mean zooplankton biomass				
			Reference	Logged-	Burned-	*F*	*P*
Cyclopoida (mg d.w.•m^{-3})		June	12	10	17	1.67	
		July	6	5	8	1.11	
		Sept	3	2	3	0.18	
Rotifera (mg d.w.•m^{-3})		June	4.4	3.1	9.0	3.13	0.06
		July	1.5	1.8	2.4	1.12	
		Sept	1.1	1.2	1.7	0.88	
Total limnoplankton (mg AFDM • m^{-3})	1996	June	66	54	85	2.00	
		July	49	55	70	1.82	
		Sept	36	30	42	1.09	
	1997	June	68	64	111	2.25	
		July	75 (a)	101 (ab)	132 (b)	6.44	0.005
		Sept	32	31	38	0.45	
	1998	June	74	64	75	0.18	
		July	36	37	44	1.14	
		Sept	62	51	47	0.68	
Crustacean size fraction (mg AFDM • m^{-3})	1996	June	14	16	21	0.79	
		July	11	14	17	1.20	
		Sept	7	7	9	0.25	
	1997	June	16	21	36	2.43	
		July	18 (a)	23 (ab)	39 (b)	4.70	0.02
		Sept	6	4	6	0.58	

Variable	Year	Sampling period	Mean zooplankton biomass				
			Reference	Logged-	Burned-	*F*	*P*
	1998	June	20	17	23	0.24	
		July	8	10	10	0.62	
		Sept	14	10	10	0.54	
Copepodite size fraction (mg AFDM • m^{-3})	1996	June	20	14	22	2.33	
		July	16	14	18	0.60	
		Sept	15	11	14	1.00	
	1997	June	20	20	30	1.02	
		July	33	35	40	0.34	
		Sept	13	12	15	0.33	
	1998	June	25	23	24	0.04	
		July	13	10	14	1.09	
		Sept	25	15	17	1.63	
Rotifer size fraction (mg AFDM • m^{-3})	1996	June	14 (ab)	11 (a)	23 (b)	3.93	0.03
		July	9	12	15	1.62	
		Sept	6	6	9	2.15	
	1997	June	17	13	26	2.38	
		July	10 (a)	24 (b)	29 (c)	7.12	0.002
		Sept	6	6	9	1.74	
	1998	June	13	12	11	0.10	
		July	7 (a)	8 (ab)	12 (b)	4.24	0.02
		Sept	11	11	10	0.08	

Variable	Year	Sampling period	Mean zooplankton biomass				
			Reference	Logged-	Burned-	*F*	*P*
Algal size fraction (mg AFDM • m^{-3})	1996	June	14	12	14	0.48	
		July	9	12	12	1.43	
		Sept	5	5	6	1.11	
	1997	June	9	8	11	1.61	
		July	8	11	7	1.30	
		Sept	5	6	5	0.31	
	1998	June	10	10	8	0.50	
		July	7	7	6	0.12	
		Sept	6	6	5	0.77	

Figure 1. Among-group differences in the 1996 average biomass of zooplankton taxonomic groups (mg d.w.•m^{-3}). From left to right, bars represent undisturbed- (white), logged- (hatched) and burned-watershed lakes (shaded). Error bars represent the 95% confidence intervals on the mean (back-calculated from log-transformed values). Bars with different letters represent groups with significantly different means (α=5%, Scheffe's multiple range test).

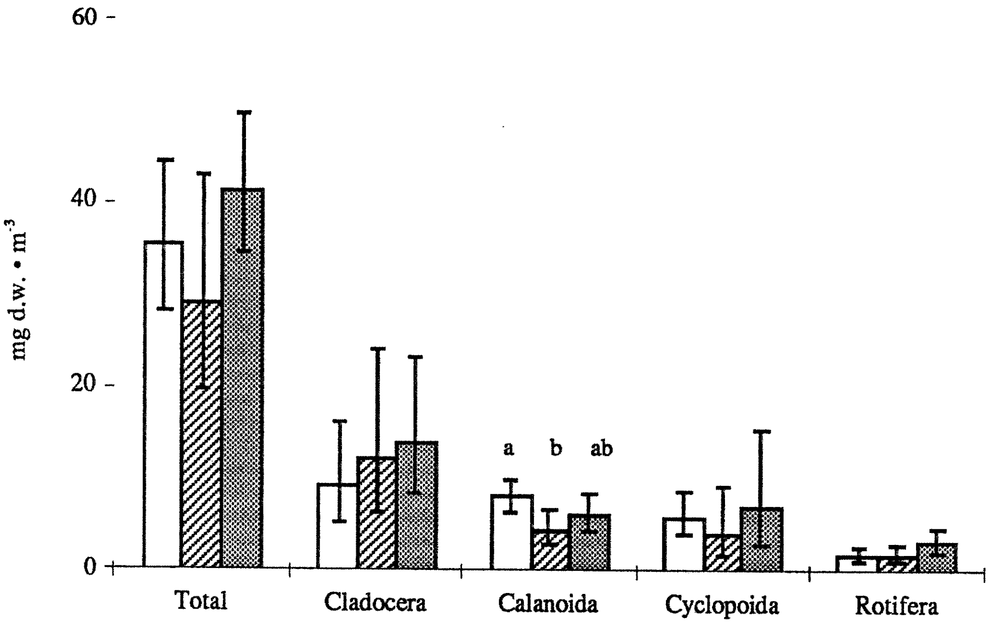
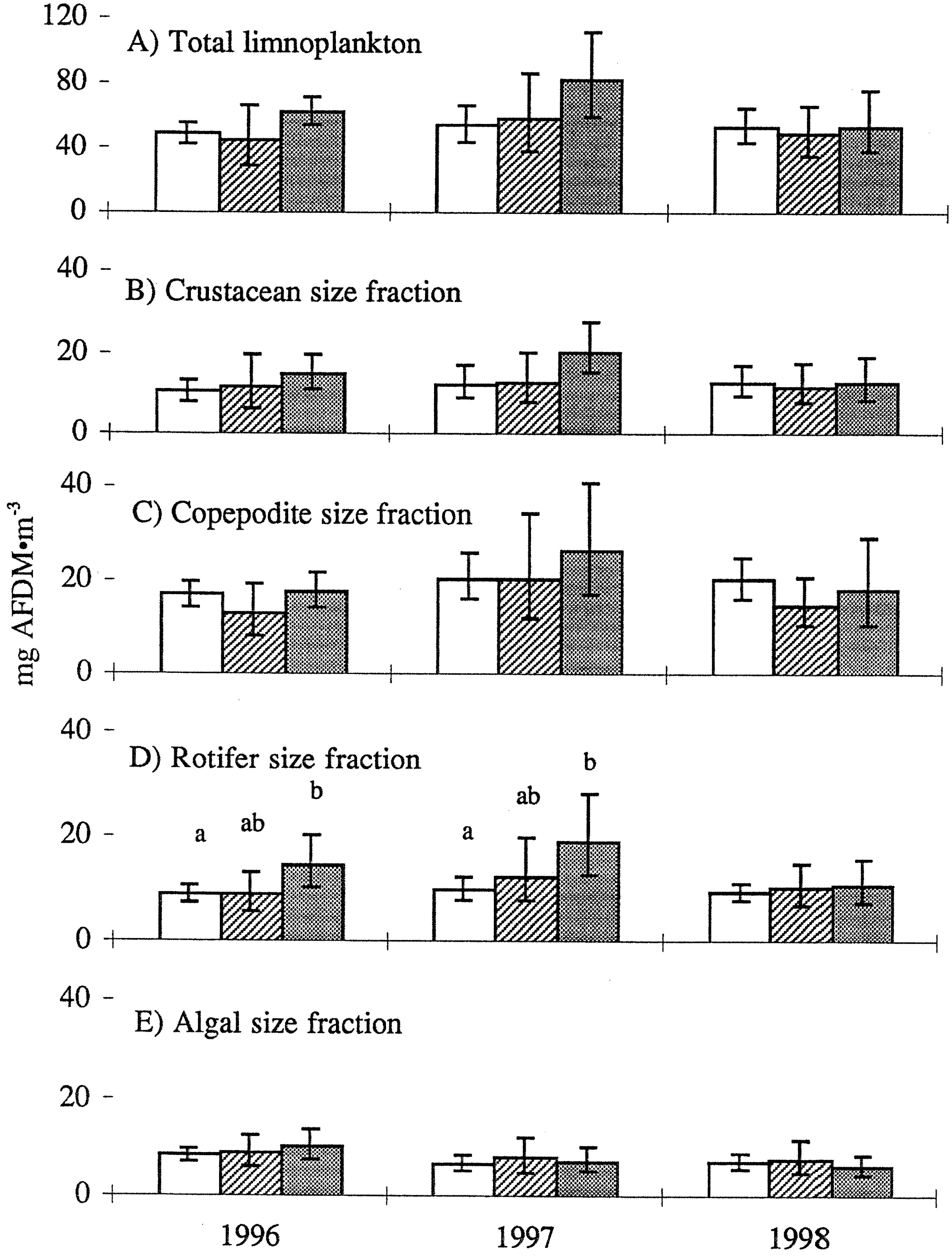
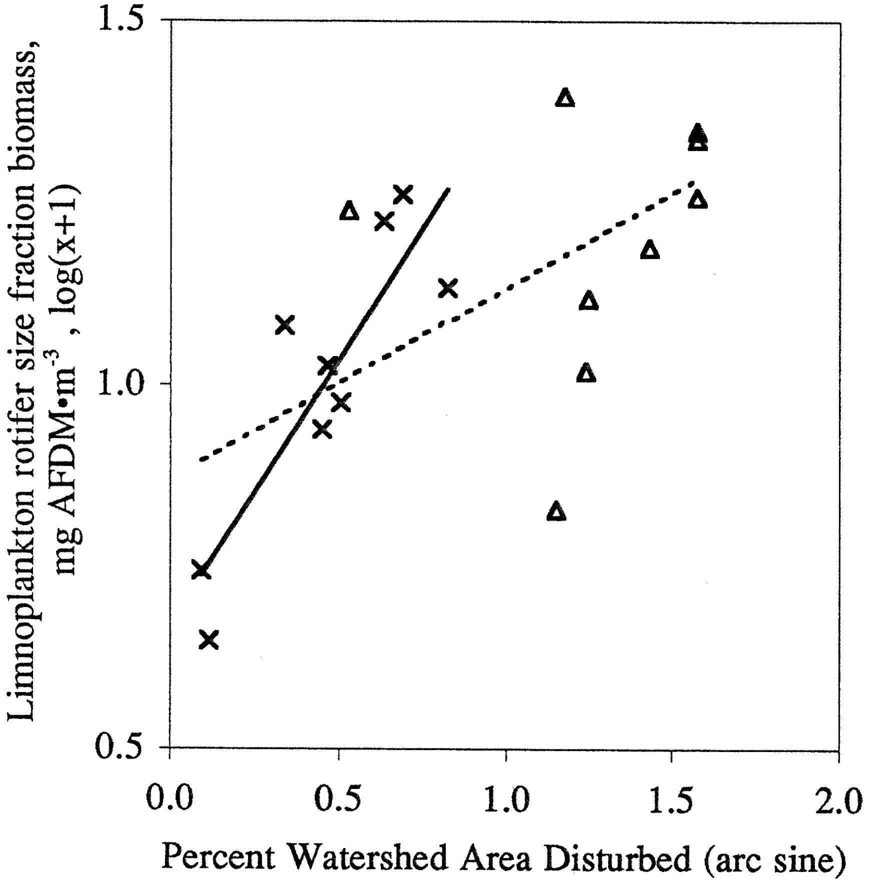


Figure 2. Among-group differences in total limnoplankton and the four size fractions during the years 1996, 1997 and 1998 (mg AFDM•m^{-3}). From left to right, bars represent undisturbed- (white), logged- (hatched) and burned-watershed lakes (shaded). Error bars represent the 95% confidence intervals on the mean (back-calculated from log-transformed values). Bars with different letters represent groups with significantly different means (α=5%, Scheffe's multiple range test). Heteroscedasticity was detected in the 1996 total limnoplankton data (X^2_2=9.34, P=0.009, Bartlett test). A non-parametric Kruskal-Wallis test (Sokal and Rohlf 1981: 405) for those data did not detect any significant among group differences (X^2_2=5.25, P=0.073).



mg AFDM•m^{-3}
A) Total limnoplankton
0
40
80
120
B) Crustacean size fraction
0
20
40
C) Copepodite size fraction
0
20
40
D) Rotifer size fraction
a
ab
b
a
ab
b
0
20
40
E) Algal size fraction
0
20
40
1996
1997
1998

Figure 3. Relationship between the biomass of the rotifer size fraction of limnoplankton (dependent variable Y) and disturbance intensity (independent variable X) one year after disturbances (1996). Logged-watershed lakes are represented by crosses, and burned-watershed lakes by triangles. Regression equation for both types of lakes (dotted line): Y = 0.26(X) + 0.87, *n*=18, *P*=0.005, r^2=40%. Regression equation for logged-watershed lakes (solid line): Y = 0.73(X) + 0.68, *n*=9, *P*=0.002, r^2=77%.



CHAPITRE II – Effects of catchment perturbations by logging and wildfires on zooplankton species richness and composition in Boreal Shield lakes

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Summary

1. Forest logging and wildfires are important perturbations of the boreal forest, but their respective effects on lake aquatic biota remain unknown. Here, we test whether zooplankton species richness and species assemblages differed among three groups of lakes in Eastern Canada characterized by different catchment conditions: logged in 1995 (*n*=9); burnt in 1995 (*n*=9); unperturbed (*n*=20). Lakes were sampled in June, July, and September one year after catchment perturbations.

2. Cumulative species richness in reference lakes averaged 46 (33 to 60) of which 63% were rotifers. Cumulative species richness and diversity in logged and burnt lakes did not differ from those in reference lakes.

3. Lake species assemblages were described by the density of 62 species (41 rotifers and 21 crustaceans). Among-group differences in species assemblages were not significant. Almost 25% of the among-lake and among-sampling date variability could be accounted for by 13 environmental factors, among which dissolved oxygen concentration and cyanobacterial biovolume were the most important. About 5% of species assemblage variability was attributed to co-variation between environmental factors and time of sampling.

4. Variations in zooplankton species richness and assemblages in Boreal Shield lakes are important, both among lakes and among sampling dates. They seem to depend on environmental factors unrelated to catchment-based perturbations, at least on the short term (one year).

Introduction

Aquatic ecosystems around the world are under pressure from a variety of environmental perturbations (Carpenter *et al.*, 1992; Schindler, 1998). In the Canadian boreal ecozone, forest clear-cutting and wildfires represent two common perturbations (Canadian Forest Service, 1998). While wildfires are a natural feature of the boreal forest, large scale forest harvesting has been present for only a century. Despite its recent occurrence in the history of the boreal forest, the surface area annually affected by logging now compares to the one burnt by forest fires: ca. 10 000 km^2 or 0.4% of the surface of productive forest in Canada (Canadian Forest Service, 1998).

Studies on the effects of logging and wildfires on aquatic ecosystems have mostly been limited to streams (reviewed in Krause, 1982). Reported effects include increases in water runoff and losses of phosphorus, nitrate, and major ions (Hobbie & Likens, 1973; Likens *et al.* 1970; Schindler *et al.*, 1980). In contrast, responses of lakes to logging and wildfires have not been as extensively studied, especially for zooplankton communities. Recent research, however, has focused on comparing the effects of logging and wildfires on water quality and aquatic biota in Boreal Shield lakes (Carignan & Steedman, 2000).

Zooplankton communities represent an important lake component because of their role in carbon flow (Hairston & Hairston, 1993), thermal stratification (Mazumder *et al.*, 1990), chlorophyll yield (Mazumder, 1994), and nutrient regeneration and stoichiometry (Vadstein *et al.*, 1995). Logging or wildfires may affect the structure and function of zooplankton communities, and subsequently lake food web structure and metabolism. The effects of logging on zooplankton density has been difficult to detect when less than 35% of the catchment area was logged (Rask *et al.*, 1998). A more recent study comparing the effects of logging and wildfires on zooplankton communities indicated there was a tendency towards increased rotifer biomass in burnt-catchment lakes, and decreased calanoid biomass in logged-catchment lakes relative to unperturbed-catchment lakes

(Patoine *et al.*, 2000). However, such biomass variations at a coarse level of taxonomic grouping could be accompanied by even greater variations at the species level. Shifts in zooplankton species assemblages have previously been related to environmental perturbations such as acid rain (Havens & Carlson, 1998; Locke, 1992; Pinel-Alloul *et al.*, 1990), chemical contamination (Havens & Hanazato, 1993), and eutrophication (Attayde & Bozelli, 1998). Furthermore, land characteristics such as land-use, geology, and recreational shoreline disturbances have also been associated with variations in species assemblages of phytoplankton (Jan Stevenson & White, 1995), phytobenthos (Leland, 1994), and zooplankton (Stemberger & Lazorchak, 1994). It is thus likely, but still unknown, that logging or wildfires could be associated with different zooplankton species assemblages.

In addition to changes in species assemblages, species richness should, on theoretical grounds, decrease in perturbed ecosystems (Odum, 1985). Indeed, decreased zooplankton species richness has been reported in lakes under certain types of environmental perturbations, namely acidification (Minns *et al.*, 1990; Havens & Carlson, 1998), eutrophication (Schindler, 1990), and copper contamination (Havens, 1994). However, the effects of logging and wildfires on zooplankton species richness in boreal lakes remains unknown to date.

The present paper is the first attempt at examining whether forest logging and wildfires have any effects on zooplankton species richness and assemblages in Quebec Boreal Shield lakes, and if so, whether the effects of the two perturbations are different. We compared zooplankton species richness and assemblages among three groups of lakes sharing similar morphometric characteristics, but differing by their catchment conditions: unperturbed, logged, or burnt. We also evaluated the effects of sampling date during summer and various environmental factors as sources of variation in zooplankton species richness and assemblages.

Material and methods

STUDY LAKES

All the lakes were situated on the Canadian Boreal Shield, surrounding Réservoir Gouin (47°52' - 48°60' N, 73°19' - 76°43' W). A complete description of landscape features, geology, climate and catchment physiography and vegetation can be found in Carignan, D'Arcy & Lamontagne (2000). Lakes were selected to have three groups with different catchment conditions. The reference group was comprised of 20 lakes with catchments undisturbed for the past 70 years. The "cut lakes" group was comprised of nine lakes with catchments clear-cut during the summer of 1995. The proportion of catchment area cut varied between 9% and 73%, and 20 m buffer zone of unharvested vegetation were left around the lakes. The "burnt lakes" group was comprised of nine lakes whose catchments had burnt during the summer of 1995. The proportion of catchment area burnt varied between 50% and 100%. The 38 lakes were selected so as to minimize differences in lake morphometry and catchment physiography among the three groups (Table 1).

SAMPLING AND ZOOPLANKTON ANALYSES

The lakes were sampled in June, July and September of 1996, roughly one year after catchment disturbances. Zooplankton was sampled at the deepest point in the lakes, established by echosounding, with a 53 μm mesh cantilevering net (Filion, Chain & Futter, 1993) from 1 m above the sediment to the lake surface. Filtered water volume varied between 80 and 1200 L depending on lake depth. Zooplankton was narcotized in the field with carbonated water and preserved in 4% formaldehyde. In the laboratory, larvae of the dipteran *Chaoborus* were removed from the samples and counted. Taxonomic analyses were performed on 10 mL sub-samples. Zooplankton was identified to the species level, following the keys of Brandlova, Brandl & Fernando (1972), Edmonson (1959), and Smith & Fernando (1978), and densities were expressed as ind.•l^{-1}. Richness was calculated as the number of species detected per lake per sampling date. Cumulative richness (total, rotifers, and crustaceans) was calculated as the number of species detected per lake, summed across the three sampling dates. The Shannon-Weaver diversity index (Legendre & Legendre, 1998: 240) was also calculated for the entire zooplankton community.

Integrated water samples for water quality, chlorophyll *a* and phytoplankton analyses were taken from the euphotic zone (1% of incident PAR) at the same site as zooplankton samples (Carignan *et al.*, 2000; Planas *et al.*, 2000). Fish were sampled in the 38 lakes over two years during the summers of 1996 and 1997 using experimental monofilament gill nets with a fishing effort varying between 6 and 12 nets par lake per night, depending on lake area (St-Onge & Magnan, 2000).

STATISTICAL ANALYSES

Richness and diversity

Differences among reference, cut, and burnt lakes in cumulative species richness and diversity were tested with a one-way analysis of variance (ANOVA), with catchment condition as the main treatment factor. Among group differences in mean monthly richness were tested with a one-way, repeated measure analysis of variance (RM-ANOVA), with catchment condition as the main treatment effect and sampling dates as repeated measurements. Among-month differences were tested by treating sampling date as the main treatment factor in one-way ANOVAs for the reference, logged, and burnt groups of lakes. Significance level was fixed at $\alpha=5\%$. Relationships between species richness and the 51 environmental variables listed in Table 2 were examined on an exploratory basis by considering those Pearson correlation coefficients that were significant at $\alpha'=0.001$ (Bonferroni correction for multiple testing, Legendre & Legendre, 1998: 18). Environmental variables were grouped in four categories: Physical-chemical, Lake and catchment morphometry, Phytoplankton community structure, and Potential predators of zooplankton.

Species assemblages and catchment condition

Average rank-frequency diagrams were established for each group of lake to see what species were the most dominant in terms of relative density. This allowed a first, qualitative evaluation of the influence of catchment condition on species assemblages.

The hypothesis that catchment condition was a significant source of variation in zooplankton species assemblages was tested by canonical correspondence analysis (CCA). In the process of CCA, a species matrix (table of species densities) is constrained to be a linear combination of the variables found in an "environmental matrix" (ter Braak, 1986). The species matrix consisted of 114 rows (representing the 38 lakes sampled three times) and 62 columns, representing the density of 62 zooplankton species. The "environmental matrix" contained 114 rows and two columns of binary variables coding for a classification criterion for catchment condition : reference (0, 1), cut (0, 0), or burnt (1, 0). The analysis is thus equivalent to a multivariate analysis of variance, with the added advantage that CCA preserves the X^2 distance among samples; the X^2 distance excludes double-zeros and is therefore suited for analysis of species data (Legendre & Legendre, 1998: 451). Furthermore, there is no upper limit to the number of species that can be anlaysed in CCA, unlike MANOVA (Legendre & Legendre, 1998: 634). To take into account the repeated sampling of the lakes, sampling date was treated as a co-variable. The covariable file consisted of 114 rows and two binary variables coding for the three sampling months: June (1, 0), July (0, 1) or September (0, 0). The statistical significance of the canonical eigenvalue (α=5%) was tested by 999 block permutations conditioned on sampling date. In the case where $P \leq 0.05$, pairwise comparisons were performed. Since there were three pairs of possible comparisons among the reference, cut-, and burnt lakes, three additional analyses were performed to determine what pairs of catchment types constituted different groups with respect to zooplankton species assemblages.

Sampling date, environmental factors, and variance partitioning

The importance of sampling date in contributing to the variability in zooplankton species assemblages was evaluated by treating the co-variable file described above as the main environmental matrix, while keeping the same species matrix. Next, to evaluate the influence of various environmental factors on zooplankton species assemblages, a separate CCA was performed for each environmental variable listed in Table 2. A forward selection procedure then allowed to develop a CCA model with multiple environmental variables, each one contributing significantly (α= 5%, 999 permutations) to the variability in species assemblages. No covariable matrix was used in these CCAs. Significance testing of canonical axes at α= 5% was performed by 999 unrestricted row permutations of the residuals of the full model. The resulting probabilities value pertained to lake and sampling date variability.

Partial CCA (Borcard, Legendre & Drapeau, 1992) was used to quantify the amount of variation in species assemblages that was strictly related to environmental variables, to sampling dates, and to catchment condition. A first partial CCA allowed to decompose the total variance of the species matrix in four fractions: 1- that related only to the environmental variables previously selected by forward selection; 2- that related only to summer variations (among sampling dates); 3- that representing joint variation between environmental variables and summer variations; 4- that left unexplained. A second partial CCA allowed for the decomposition of total variance into an environmental fraction, a fraction related to catchment condition only (not co-varying with environmental variables), a fraction representing co-variation between environmental variables and catchment condition, and a fraction of unexplained variation. Preliminary correspondence analyses showed that the lake ordination was highly unbalanced and non interpretable when using untransformed data. Hence, all analyses were performed on the log(x+1) transformed values of zooplankton species densities and environmental variables with the program CANOCO (ter Braak, 1988) version 3.11 for Macintosh.

Results

LAKE AND CATCHMENT CHARACTERISTICS

Details on lake morphometry, water quality, and catchment physiography can be found in Carignan *et al.* (2000). In short, there were no significant among-group differences in lake area, maximum depth, and drainage ratio (catchment area over lake area), though maximum depth and drainage ratio tended to be higher in burnt and cut lakes than in reference lakes (Table 1). Total phosphorus (TP) concentration was higher by 40% and 56% in cut and burnt lakes respectively relative to reference lakes. Dissolved organic carbon was higher by 57% in cut lakes than in reference lakes. Alkalinity and pH did not differ among groups of lakes (Carignan *et al.*, 2000). Chlorophyll *a* concentration was higher in cut and burnt lakes (Planas *et al.*, 2000).

RICHNESS AND DIVERSITY

A total of 150 zooplankton species were identified in the 114 samples representing the 38 lakes sampled three times. Almost half (46%) of these species were common to the three catchment types (reference, cut, and burnt). More species were identified in the reference lakes (121) than in the cut (96) or burnt (106) lakes, in part because the reference group contained more lakes.

Cumulative richness in reference lakes averaged 46 (range of 33 to 60) (Figure 1A). Although mean richness in cut and burnt lakes was higher by 10% relative to reference lakes, this difference was not significant ($F_{2,35}$=2.05, P=0.15). Rotifers represented on average 63% of the total species richness, with values varying between 18 and 43 in reference lakes (Figure 1B). Cumulative rotifer richness thus showed a similar pattern of among-group variations as total zooplankton, with higher values in logged and burnt lakes relative to reference lakes; here again, though, among-group variations were not significant ($F_{2,35}$=2.27, P=0.12). Crustacean cumulative richness in reference lakes varied between 12 and 22, with a mean of 17. Among-group differences were not significant ($F_{2,35}$=0.41, P=0.67) (Figure 1C). Cumulative diversity in reference lakes averaged 2.52 (1.98 to 2.95) (Figure 1D). Ranges of variations in cut and burnt lakes were similar to those in reference lakes, and means were not statistically different ($F_{2,35}$=1.28, P=0.29). Mean monthly diversity did not differ among groups of lakes (RM-ANOVA, $F_{2,35}$=2.07, P=0.14).

Monthly richness was lower than cumulative richness by 37% (Figure 1A, B, C), suggesting different species assemblages between summer months. Monthly richness averaged 29 in reference lakes, with rotifers contributing 62%, and crustaceans 38% (Figure 1A, B, C). Among-group variations in monthly richness (total, rotifer, crustacean) were not significant (RM-ANOVA, $F_{2,35} < 2.3$, $P > 0.10$) (Figure 1A, B, C).

Among-month variations in total richness, rotifer richness, and crustacean richness were not significant in the case of reference lakes, cut lakes, and burnt lakes (all P>0.07).

Relationships between zooplankton species richness and environmental variables were examined on an exploratory basis. None of the 51 environmental factors listed in Table 2 were significantly correlated to the cumulative richness of rotifers or crustaceans, once the Bonferonni correction was applied (α'=0.001).

IMPACT OF CATCHMENT CONDITION ON SPECIES ASSEMBLAGES

Among the 150 species identified in all samples, 62 were found with an occurrence greater than 5% (41 rotifers and 21 crustaceans) and were used in the analyses which follow. All of these species were found in the three lake types. The most common species were the rotifers *Kellicotia longispina, Keratella cochlearis, Conochilus unicornis, Polyarthra remata* and *P. vulgaris*, which were found in greater than 95% of the samples. Rotifers accounted for most (90%) of total zooplankton density. In fact, among the 41 species of rotifers, only 10 were necessary to represent, on average, 75% of total zooplankton density in reference lakes (Figure 2A). The rotifer *Keratella cochlearis* was the most dominant species in reference lakes, accounting on average for 21% of total zooplankton density (rotifers and crustaceans) (Figure 2A). It was followed by *Kellicotia longispina*, *Conochilus unicornis*, and other rotifers. Ranking of rotifer species according to their relative density in cut and burnt lakes followed closely that observed in reference lakes (Figure 2A). In contrast to rotifers, the 21 species of crustaceans together accounted for barely more than 10% of total zooplankton density (Figure 2B). The calanoid *Leptodiaptomus minutus* was the crustacean species generally found with the highest relative density in reference lakes. It was followed by cladocerans of the bosminid family, and the cladocerans *Holopedium gibberum*, *Daphnia longiremis*, and *Daphnia catawba*. Other cladocerans, calanoids, and cyclopoids species followed with relative densities of lower than 1%. As was the case for rotifers, the ranking of species was similar in reference, cut, and burnt lakes (Figure 2B). Coefficients of variation for each species of rotifer and crustacean was greater than 100% in reference, cut, and the burnt groups of lakes.

Catchment condition was a significant source of variation in zooplankton species assemblages among the reference, cut, and burnt lakes (P = 0.048, Table 3). The low percentage of variance in the species matrix that was explained by catchment condition (3.0%) suggests high within group variation in species assemblages, as was already indicated in Figure 2. CCAs performed on pairs of catchment groups revealed that the zooplankton species assemblages in burnt lakes differed from that of reference lakes (P = 0.033) (Table 4). There were no statistically significant differences in the zooplankton species assemblages between reference and logged lakes (P = 0.127), nor between logged and burnt lakes (P = 0.556) (Table 3). Because the above probability value associated with the effect of catchment condition (P=0.048) was bordering the significance level of 0.05, we present hereafter additional analyses to confirm or refute it.

When CCA analyses were performed on average density values (species matrix with 38 rows), the probability value associated with the null hypothesis was 0.083 (Table 4). When CCAs were performed for each sampling date separately, catchment condition was a non-significant source of variation in June (*P*=0.16), July (*P*=0.190) and September (*P*=0.635) (Table 3). When the probabilities associated with each sampling date were combined to obtain a single probability value representing the three sampling dates (Fisher's method for combining probabilities of independent tests: Sokal and Rohlf 1981: 779), a value of *P*=0.25 was obtained. In short, the evidence indicated that catchment condition was not a significant source of variation in zooplankton species assemblages.

IMPACT OF SAMPLING DATE ON SPECIES ASSEMBLAGES

In contrast to catchment condition, the influence of sampling date was highly significant (*P*=0.001), and explained 9.5% of the variance in species assemblages. Shifts in species assemblages among the three sampling dates are illustrated in a species-environment biplot (Figure 3B). In June, we find, among other species, two large predator cylopoids *Cyclops scutifer* (abbreviated Cysc on the biplot) and *Mesocyclops edax* (Meed) with the rotifer *Keratella hiemalis* (Kehi) in greater relative density than in July or September. “July species” included the cladoceran *Daphnia dubia* (Dadu) and the predacious rotifer *Asplanchna priodonta* (Aspr) as well as the small cyclopoid *Tropocyclops prasinus* (Trpr); “September species” included the cladocerans *Daphnia schodleri* (Dasc), *Diaphanosoma brachyurum* (Dibr) and the rotifer *Polyarthra sulcata* (Posu) et *Trichocerca rousseleti* (Trro). The greater influence of sampling date on zooplankton species assemblages in comparison to catchment condition is clearly illustrated by differences in the loading of species vector on canonical axes: from relatively small in the case of the sample ordination constrained by catchment condition (Figure 3A), it increased when the ordination was constrained by sampling date (Figure 3B).

INFLUENCE OF ENVIRONMENTAL FACTORS ON SPECIES ASSEMBLAGES

Since there were no differences in species assemblages among reference, cut and burnt lakes, relationships with the environmental factors listed in Table 2 were analyzed for the entire data set, rather than for each group of lakes separately. Among the 51 environmental variables examined, dissolved oxygen concentration was the most important with 3.3% of explained variance in zooplankton species assemblages (P=0.001) (Table 2). The next best variable was the biovolume of cyanobacteria, with 2.9% (P=0.001). It was followed by catchment condition with 2.7% (P=0.001). Note that this probability value is here inadequate to test the hypothesis that catchment condition is a significant source of variability in zooplankton species assemblages because, contrary to the previous CCAs, it does not take into account the fact that the same units of observation (lakes) were repeatedly sampled. All the other environmental variables were less important than catchment condition in their ability to account for variability in zooplankton species assemblages among lakes and among dates (Table 2). When catchment condition was expressed as a continuous variable (% catchment area disturbed by logging or burning) the amount of variance explained decreased to 1.5%.

The forward selection procedure selected 13 of the 51 environmental variables (Table 2). Selected variables were of the type Physical-chemical, Phytoplankton community structure, and Potential predators; none were of the type Lake and catchment morphometry, though most of them were significant when considered alone (Table 2). Together, the selected variables could explain 23.4% of the variance in the species matrix (P = 0.01). The first two canonical axes captured 4.5% (P = 0.010) and 4.0% (P = 0.010) respectively of the total variance. The distribution of the 114 zooplankton communities (samples) in the plane of the first two canonical axes can be interpreted following two dual environmental gradients that are largely independent from one another (Figure 4C). The first gradient is illustrated by the dual oxygen concentration-cyanobacterial biovolume inverse gradient. Samples near the tip of the O2 vector (high lake oxygen concentration, low cyanobacteria biovolume) were mostly from the June sampling date (Figure 4B and C), and were characterized by higher relative densities of *Asplanchna herricki* (Ashe), Rotifera sp. (Rosp), the cladoceran *Daphnia galeata mendotae* (Dame), and the cyclopoids *Mesocyclops edax* (Meed), *M. leuckarti* (Mele). Samples near the tip of the Cyano vector (low lake oxygen concentration, high cyanobacteria biovolume) were mostly from the September sampling date (Figure 4B and C), and were characterized by a different species assemblage. Hence, sample ordination along these environmental gradients suggests a seasonal shift in species from June to September that was concomitant with a decrease in dissolved oxygen concentration, and an increase in cyanobacteria biovolume. The month to month variations in oxygen concentration and cyanobacteria biovolume suggested by the sample ordination and the species-environment biplot (Figure 4B and C) were confirmed by monthly averages of these variables (Table 4): average oxygen concentration was higher in June than in September (8.9 and 5.3 $mg \cdot l^{-1}$ respectively), while cyanobacterial biovolume was higher in September than in June (105 and 17 $\mu m^3 \cdot l^{-1}$).

The second gradient is illustrated by the dual white sucker density-chrysophyte biovolume (Caco/Chryso vectors) inverse gradient. The orientation of the Chryso vector (Figure 4C) opposite to the July samples (Figure 4B) suggests low chrysophyte biovolume during the July sampling date. This was confirmed by monthly averages of chrysophyte biovolume: from 600 $\mu m^3 \cdot l^{-1}$ in June, it decreased to 394 $\mu m^3 \cdot l^{-1}$ in July, and increased thereafter to attain 785 $\mu m^3 \cdot l^{-1}$ in September (Table 4). Orientation of the ammonium concentration (NH4), and Chlorophyte biovolume (Chloro) vectors away from the July samples can be interpreted in a similar way (Table 4). The orientation of the Caco vector towards July samples, however, cannot be interpreted with respect to sampling date because fish were sampled over two years. Fish vectors must therefore be interpreted solely as a function of lake to lake variations in fish density that are concomitant with variations in zooplankton species assemblages. Hence, samples near the tip of the Caco vector (lakes with high white sucker density), or away from the Pefl vector (lakes with low yellow perch density) were characterized by higher relative densities of the cladocerans *Daphnia pulex* (Dapu), *D. dubia* (Dadu), *Diaphanosoma leuchtenbergianum* (Dile), the calanoids *Aglaodiaptomus spatulocrenatus* (Agsp), *Epischura lacustris* (Epla), and the cyclopoid *Diacyclops bicuspidatus thomasi* (Dith), (Figure 4C). No zooplankton specimens were found in white sucker stomachs, but represented on average 25% of the stomach content of yellow perch, on a dry mass basis (average based on 1302 yellow perch specimens, P. Magnan, Université du Québec à Trois-Rivières, Canada, personal communication).

RELATIVE IMPORTANCE OF SUMMER SEASONALITY AND CATCHMENT CONDITION ON ZOOPLANKTON SPECIES ASSEMBLAGES

It is clear in the way zooplankton communities tended to cluster according to sampling date when constrained by environmental variables (Figure 4B) that a fraction of the variance in zooplankton species assemblages explained by the 13 environmental variables reflected month to month variations rather than lake to lake variation. The amount of variation in zooplankton species assemblages that represented co-variation between sampling date and the 13 environmental variables amounted to 5.4% (Figure 5A). Hence, the amount of "purely" temporal variation (i.e. not co-varying with the set of 13 environmental variables) was 4.1% ($P < 0.005$), and the amount of "purely" environmental variation was 18.0% ($P < 0.005$). In other words, the ordination of the 114 samples shown in Figure 4B is more a function of among lake gradients in environmental conditions than a temporal gradient.

In contrast, there was no apparent tendency for zooplankton communities to cluster according to catchment type when constrained by environmental variables (Figure 4A), suggesting lakes belonging to different catchment types could share similar environmental characteristics or, more precisely, similar combinations of those environmental variables represented by canonical axes I and II (listed in Table 4). Partial CCA allowed to quantify the fraction of environmental variation that was correlated with catchment condition. The amount of variation that could jointly be explained by the 13 environmental variables and catchment condition amounted to 1.0% (Figure 5B). The amount of variance that could be explained by catchment condition alone, independently of the 13 environmental variables amounted to 1.7% and was not significant (*P* = 0.20). The 22.4% of variance associated with the 13 environmental variables independently of catchment condition remained significant (*P* = 0.010).

In short, among-lake variations in dissolved oxygen and nutrient concentration (TP, ammonium), algal biovolume (cyanobacteria, chrysosphytes, chlorophytes), and fish density (white sucker, yellow perch) were the most important sources of variation in zooplankton species assemblages. Month of sampling was the second most important source of variation in species assemblages; it likely played the role of a surrogate for other environmental factors, strongly correlated to month of sampling, but not measured in this study (cf. Discussion). Last, catchment condition was a non-significant source of variation in species assemblages.

Discussion

The evidence presented here has not allowed us to detect a short-term effect of logging and wildfires on zooplankton species richness, diversity or assemblages in Canadian Boreal Shield lakes. Species identified here were previously reported in other Canadian Shield lakes (Arnott, Magnusson & Yan, 1997; Carter *et al.*, 1980; Keller & Pitblado, 1989; Pinel-Alloul, Niyosenga & Legendre, 1995). Monthly species richness values were comparable to those reported in Arnott *et al.* (1997), Keller & Conlon (1994), Patalas & Salki (1993), and Stemberger *et al.* (1996). The absence of among-month differences in species richness and the increase in cumulative relative to single-month richness is also consistent with results by Arnott *et al.* (1997).

On theoretical grounds, community species richness is predicted to decrease in the presence of environmental stress (Odum, 1985). Zooplankton species richness has indeed been found to decrease under certain types of environmental perturbations, for example acidification stress (Locke & Sprules, 1994). With respect to catchment perturbations, Stemberger & Lazorchak (1994) found that zooplankton richness, especially that of microzooplankton (48-202 μm), was positively related to the percentage of shoreline disturbance in 19 New-England lakes, which is unexpected with regards to Odum's predictions. Similarly, in the present study, there was a tendency for rotifer species richness values to be higher in cut and burnt lakes relative to reference lakes, though mean differences were not significant. Hence the evidence was not convincing that catchment perturbations was associated with decreases in zooplankton species richness.

Two alternative conclusions can be drawn from the lack of demonstrated differences in zooplankton species richness and assemblages among reference, cut, and burnt lakes, one year after perturbations. First, the change in the zooplankton's habitat among groups of lakes may not have been important enough to result in different zooplankton species assemblages. Even though among-group differences in basic chemical characteristics such as TP, TN, chl-*a*, alkalinity and DOC were significant, they were less than two-fold relative to reference lakes (Carignan *et al.*, 2000). Furthermore, among-group differences in acidity, a well known factor influencing species assemblages (Carter *et al.*, 1986; MacIsaac, Hutchinson & Keller, 1987; Pinel-Alloul *et al.*, 1990; Sarvala & Halsinaho, 1990), were less than 50-fold, and not significant (Carignan *et al.*, 2000). Zooplankton species assemblages may naturally tolerate such small variations of these properties in their habitat. In contrast, environmental sources of stress associated with different zooplankton species assemblages often pertain to continuous variables, rather than class variables, with ranges of variation as great as 20-fold in the case of TP and chl-*a* (Attayde & Bozelli, 1998), or greater than 1000-fold in the case of acidification (MacIsaac *et al.*, 1987).

Second, ecologically significant changes in the species assemblages that would be related to catchment condition may take several years to develop. Given the generation time of rotifers spans several days and that of crustaceans several months (Wetzel, 1983: 442), there may be insufficient time in a year for community structure to adapt to the new environment. Logging could, in fact, have indirect and longer-term effects on the zooplankton species richness and species assemblages. For example, the road construction necessary to forestry activities opens up new territories and can lead to an increase in fishing activity in previously inaccessible lakes (Gunn & Sein, 2000). Increased fishing activity could, in turn, change zooplankton community structure.

One should also consider the possibility that the observed among-group variations in species richness, species diversity and species assemblages do represent, in fact, true differences. Indeed, the lack of statistically significant differences among groups of lakes could be the result of insufficient statistical power. It is clear that reference lakes alone presented a great deal of variability in species richness, diversity and assemblages. Hence, a true among-group variation in zooplankton community structure would have required more lakes per group for the observed variations to be declared statistically significant at the 5% level. It is questionable, however, whether the small among-group variations that have been observed in species richness, species diversity and species assemblages would represent ecologically significant differences.

INFLUENCE OF OXYGEN, CYANOBACTERIA, AND TIME OF THE SEASON

Dissolved oxygen concentration and cyanobacterial biovolume have never been reported before as important sources of variation in zooplankton species assemblages of boreal lakes. Here, they appeared more important than other environmental factors previously reported as significant in accounting for among-lake variations in zooplankton species assemblages, such as pH, and the concentration of major ions, TP, and chl-*a* (MacIsaac *et al.*, 1987; Pinel-Alloul & Pont, 1991; Stemberger and Lazorchak, 1994).

These studies, however, did not include dissolved oxygen concentration nor cyanobacterial biovolume as environmental factors. Most important, these studies aimed at examining the factors associated solely with among-lake variation in zooplankton species assemblages. In contrast, the present study considered both among-lake and among-month variations. This may in part explain why seasonally dynamic variables such as oxygen concentration and cyanobacterial biovolume were here important in explaining variability in species assemblages. Oxygen concentration is a known factor influencing the vertical distribution of some species of zooplankton within a lake, in part for the role it plays in creating a refuge for *Daphnia* against planktivorous fish (Hanazato, 1992), or for hypolimnetic species (Armengol, Esparcia & Miracle, 1998). We can only speculate on the role oxygen played in the observed among-lake distribution of zooplankton species because we did not survey the vertical distribution of zooplankton species in the water column. With respect to cyanobacteria, they represent a poor food source for some species of crustaceans (DeBernardi & Giussani, 1990). In the present study, however, cyanobacteria were of minor importance relative to total phytoplankton biomass (Planas *et al.*, 2000) and it is unclear how they could have exerted constraints on food resources for zooplankton, even during September when they reached their maximum of biomass. The inverse correlation observed between lake oxygen concentration and cyanobacterial biovolume is consistent with observations by Trimbee & Prepas (1988) who showed that lakes with a greater proportion of the water column well oxygenated (> 2 mg•l^{-1}) have low relative biomass of blue-green algae.

The 5% of variability in species assemblages associated with sampling date alone can conceivably represent one or more environmental gradients temporally structured, but not measured in this study. For example, the bacteria community can show marked seasonal variations and play an important role in the bottom-up control of rotifers (Rublee & Bettez, 1995).

INFLUENCE OF WHITE SUCKER AND YELLOW PERCH

Yellow perch is a known planktivorous fish whose presence can be associated with small-sized zooplankton communities and the absence of *Daphnia pulex* relative to yellow perch-free lakes (Galbraith, 1967). Here, yellow perch density was negatively associated with *Daphnia pulex*, thus supporting previously reported trends between fish and zooplankton communities.

The role of white sucker, however, is not as clear as that of yellow perch since zooplankton was not a part of white sucker's diet. The presence of white sucker, however, can result in a shift in the diet of brook trout from zoobenthos to zooplankton, relative to allopatric brook trout populations (Lacasse & Magnan, 1992). Under such a scenario, increasing white sucker density would have been associated with smaller zooplankton species. Observations, though, were contrary to such a scenario since increasing white sucker density was associated with typically large zooplankton specimens such as *Daphnia pulex*, and *Epischura lacustris*. Furthermore, the importance of brook trout in structuring zooplankton communities in the present study was probably weak since it occurred in only eight lakes, six of which contained white sucker. The role of white sucker in accounting for variability in zooplankton species assemblages remains unclear for the moment.

INFLUENCE OF LAKE AND CATCHMENT MORPHOMETRY

Environmental factors related to lake and catchment morphometry are often correlated with zooplankton species composition of North-American lakes, especially maximum depth and lake area (Keller & Conlon, 1994; Patalas, 1971). Consistent with these previous studies, lake area was here an important morphometric variable correlated to among-lake variations in zooplankton species associations. However, none of the 10 morphometric variables examined were selected as a significant correlate when presented with the other types of environmental variables, suggesting water quality and biotic factors were relatively more important in accounting for variability in zooplankton species assemblages. The greater influence of factors related to water chemistry, phytoplankton community structure, and fish community structure relative to morphometric factors has previously been demonstrated for zooplankton communities in Laurentian Shield lakes (Pinel-Alloul *et al.*, 1995).

INFLUENCE OF THE DURATION OF CATCHMENT PERTURBATIONS

Few studies have examined the influence of catchment perturbations on plankton community structure. Stemberger & Lazorchak (1994) showed that shoreline disturbance was one among six environmental variables that accounted for among-lake variations in zooplankton community structure of 19 New-England lakes. The approach used by these authors, however, was to collapse the 113 species identified into 12 groups defined on the basis of taxonomy, body size, life-history stages, and feeding modes. Such an approach may have been more adequate to examine relationships with environmental disturbances than analysis of species-based data. More fundamentally, however, shoreline disturbance may not be comparable to catchment deforestation by logging or burning. Shoreline disturbance, defined as the percentage of lake shoreline with docks, access sites, boat houses, swimming beaches, buildings, lawns, roads etc. (Stemberger & Lazorchak, 1994), is a type of disturbance usually applied more or less continuously through time, over many years. The zooplankton species assemblages, along with the other components of the ecosystem, therefore dispose of several years to change in response to these perturbations. In contrast, logging and forest fires are transient in time, lasting less than one year. As a result, insufficient time may have elapsed between the moment of perturbations and the moment of zooplankton sampling for extensive changes in species assemblages to have taken place in response to the perturbations.

In conclusion, variations in zooplankton species richness and assemblages in Boreal Shield lakes in Québec are important, both among lakes and among sampling dates, and seem to depend on environmental factors unrelated to catchment-based perturbations, at least on the short term. A taxonomic approach to zooplankton community structure may be inadequate to assess the impacts of catchment-based perturbations, one year after perturbations. A sized-based approach, as advocated by Sprules & Holtby (1979), or the grouping of species in functional groups, as practiced by Stemberger and Lazorchak (1994) may prove better suited to detect trends between zooplankton community structure and environmental perturbations. Alternatively, shifts in species assemblages related to catchment-based perturbations may take several years before becoming apparent.

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Table 1. Mean values of selected limnological variables for the three groups of lakes under study (with minimum and maximum values), one year after watershed perturbations. Significant among-group differences are indicated by different lower capitals letter. Based on Carignan *et al.* (2000), except chlorophyll *a*, based on Planas *et al.* (2000).

	Reference (*n*=20)	Logged (*n*=9)	Burned (*n*=9)
Percent Watershed Area Perturbed	0% (0%-1%)	47% (9%-73%)	91% (50%-100%)
Maximum Depth (m)	12.5 (7-21)	14.0 (5-30)	17.0 (10-34)
Lake Area (ha)	44 (14-81)	56 (18-231)	40 (17-64)
Drainage Ratio (Drainage area/Lake area)	5.2 (2.3-15.4)	6.7 (2.0–13.2)	7.1 (2.5–11.6)
pH	6.2 (5.8-7.0)	6.7 (5.7-7.2)	6.5 (6.0-7.0)
Total phosphorus ($\mu g \cdot L^{-1}$)	7.0 (4.9-11.8) a	9.8 (5.6-15.8) b	10.9 (5.6-17.3) b
Dissolved organic carbon ($mg \cdot L^{-1}$)	5.1 (2.8-9.2) a	8.0 (3.0-13.3) b	5.6 (3.1-8.0) ab
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	1.9 (0.9-3.2) a	2.4 (1.6-3.3) b	3.1 (1.7-4.2) b

Table 2. List of the 51 environmental variables examined, and selected as explanatory factors of zooplankton species assemblages variability in CCAs, with the percentage of explained variance and associated probability (see Figure 4).

Type of variable	Environmental variable	Percent variance explained	*P*	Selected by the forward selection
Physical and chemical	Temperature of epilimnion (°C)	1.2%	0.073	
	Average water column oxygen concentration (mg•L^{-1})	3.3%	0.001	√
	Dissolved organic carbon (mg•L^{-1})	2.2%	0.001	
	Total phosphorus (µg•L^{-1})	2.0%	0.001	√
	Total nitrogen (µg•L^{-1})	1.6%	0.007	
	Nitrate (µg•L^{-1})	1.9%	0.001	
	Ammonium (µg•L^{-1})	2.6%	0.001	√
	pH	2.2%	0.001	
	Alkalinity (µeq•L^{-1})	2.2%	0.001	
	Chloride (mg•L^{-1})	1.6%	0.002	
	Sulfate (mg•L^{-1})	1.1%	0.110	
	Calcium (mg•L^{-1})	2.4%	0.001	√
	Magnesium (mg•L^{-1})	2.2%	0.001	√
	Sodium (mg•L^{-1})	1.7%	0.002	
	Potassium (mg•L^{-1})	1.8%	0.002	
	Chlorophyll *a* (µg•L^{-1})	1.6%	0.003	
Lake and catchment morphometry	Lake area (km^2)	1.7%	0.003	
	Total area of upland lakes (km^2)	0.9%	0.354	
	Drainage area (km^2)	1.4%	0.029	
	Drainage ratio	2.1%	0.001	
	Altitude (m)	1.5%	0.009	
	Lake perimeter (km)	1.0%	0.242	
	Shoreline development	0.9%	0.475	
	Water residence time (year)	2.0%	0.001	
	Watershed condition (binary variable)	2.7%	0.001	
	% watershed area disturbed (km^2•km^{-2})	1.5%	0.002	

Type of variable	Environmental variable	Percent variance explained	*P*	Selected by the forward selection
Phytoplankton community structure	Algal richness (number of species per lake)	1.2%	0.065	
	Cyanophyte biovolume ($\mu m^3 \bullet L^{-1}$)	2.9%	0.001	√
	Cryptophyte biovolume ($\mu m^3 \bullet L^{-1}$)	1.9%	0.002	
	Diatom biovolume ($\mu m^3 \bullet L^{-1}$)	1.2%	0.047	
	Dinoflagellates ($\mu m^3 \bullet L^{-1}$)	0.9%	0.357	
	Chlorophyte biovolume ($\mu m^3 \bullet L^{-1}$)	1.9%	0.001	√
	Chrysophyte biovolume ($\mu m^3 \bullet L^{-1}$)	2.3%	0.001	√
	Euglenophyte biovolume ($\mu m^3 \bullet L^{-1}$)	1.0%	0.255	
	Total phytoplankton biovolume ($\mu m^3 \bullet L^{-1}$)	1.6%	0.004	
Potential predators of zooplankton	*Chaoborus* density (ind.$\bullet m^{-3}$)	1.2%	0.069	
	White sucker (*Catostomus commersoni*) CPUE	2.0%	0.001	√
	Northern pike (*Esox lucius*) CPUE	1.9%	0.001	
	Yellow perch (*Perca flavescens*) CPUE	1.4%	0.011	√
	Lake whitefish (*Coregonus clupeaformis*) CPUE	0.8%	0.565	
	Fallfish (*Semotilus corporalis*) CPUE	0.8%	0.688	
	Walleye (*Stizostedion vitreum*) CPUE	1.2%	0.064	√
	Burbot (*Lota lota*) CPUE	0.8%	0.603	
	Brook trout (*Salvelinus fontinalis*) CPUE	1.3%	0.046	
	Pearl dace (*Semotilus margarita*) CPUE	1.4%	0.027	√
	Unknown fish sp. no. 1 CPUE	0.8%	0.609	
	Lake chub (*Couesius plumbeus*) CPUE	1.3%	0.044	
	Golden shiner (*Notemigonus crysoleucas*) CPUE	1.2%	0.068	√
	Unknown fish sp. no. 0 CPUE	0.8%	0.737	
	Finescale dace (*Chrosomus neogaeus*)* CPUE	1.4%	0.015	
	Unknown fish sp. no. 2 CPUE	0.8%	0.597	

* Previously *Phoxinus neogaeus* (Cope)

Table 3. Results of canonical correspondence analyses of the zooplankton species matrix with catchment condition. Rows refer to different analyses. Row 1: among-group differences (reference, cut, and burnt lakes). Rows 2, 3, 4: pairwise comparisons of groups. Row 5: among-group differences, based on average density values. Rows 6, 7, 8: among-group differences by sampling date. The Percent variance explained represents the ratio of the sum of canonical eigenvalues over the sum of all eigenvalues, once the variance associated with the covariable (sampling date) has been removed. *P* is the probability that the percentage variance explained does not differ from that corresponding to the random association of the two matrices.

Row no.	Species matrix Y	Covariable matrix	Percent variance explained by catchment condition	*P*
1	Ref., logged, and burnt	Sampling date	3.0%	0.048
2	Ref. vs. logged	Sampling date	2.0%	0.127
3	Ref. vs burnt	Sampling date	2.3%	0.033
4	Logged vs. burnt	Sampling date	2.3%	0.556
5	Ref., logged and burnt, average values	None	6.7%	0.083
6	Ref., logged and burnt in June	None	6.1%	0.16
7	Ref., logged & burnt in July	None	6.1%	0.190
8	Ref., logged & burnt in Sept.	None	5.1%	0.635

Table 4. Mean values (min-max) for the variables selected in the CCA of zooplankton species assemblages, by catchment condition, and by sampling period. Variables 1 to 5 based on Carignan *et al.* (2000); variables 6 to 8 based on Planas *et al.* (2000). Fish (variables 9 to 12) were sampled once in each lake over a two year period, so no statistics are presented by sampling period (based on St-Onge & Magnan, 2000).

	Environmental variable	Reference group of lakes (*n*=60 samples)	Logged group of lakes (*n*=27 samples)	Burned group of lakes (*n*=27 samples)	June samples (*n*=38)	July samples (*n*=38)	Sept. samples (*n*=38)
01	Oxygen concentration (mg•L^{-1})	7.1 (2.9–11.1)	7.0 (3.5–10.7)	6.9 (3.4–10.6)	8.9 (6.4–11.1)	6.9 (5.0–8.9)	5.3 (2.9–8.7)
02	Total Phosphorus (µg•L^{-1})	7.0 (4.4–15.5)	9.8 (5.3–19.6)	10.9 (4.7–25.4)	9.1 (4.6–25.4)	9.0 (5.2–19.6)	7.7 (4.4–16.0)
03	Ammonium (µg•L^{-1})	5.4 (0–14.4)	6.1 (0.2–13.3)	7.6 (0.6–16.4)	9.0 (3.8–16.4)	3.6 (0–9.7)	5.6 (2.1–14.4)
04	Calcium (µg•L^{-1})	1.5 (1.0–2.6)	1.5 (1.0–2.3)	2.2 (1.4–3.1)	1.6 (1.0–2.9)	1.6 (1.0–2.9)	1.7 (1.0–3.1)
05	Magnesium (µg•L^{-1})	0.4 (0.2–0.7)	0.4 (0.2–0.7)	0.7 (0.5–0.9)	0.5 (0.2–0.9)	0.5 (0.2–0.9)	0.5 (0.3–0.9)
06	Cyanobacterial biovolume (µg w.w. •L^{-1})	55 (2–226)	52 (1–334)	46 (0–204)	17 (0–104)	33 (0–183)	105 (10–334)
07	Chrysophyte biovolume (µg w.w. •L^{-1})	530 (39–9570)	572 (49–2550)	753 (137–3483)	600 (213–2198)	394 (39–3843)	785 (70–9570)
08	Chlorophyte biovolume (µg w.w. •L^{-1})	134 (15–674)	123 (9–250)	211 (4–1925)	201 (48–1925)	97 (4–520)	152 (11–758)
09	White sucker CPUE	6 (0–36)	4 (0–21)	3 (0–9)			

	Environmental variable	Reference group of lakes (n=60 samples)	Logged group of lakes (n=27 samples)	Burned group of lakes (n=27 samples)	June samples (n=38)	July samples (n=38)	Sept. samples (n=38)
10	Yellow perch CPUE	14 (0–133)	6 (0–13)	5 (0–18)			
11	Pearl dace CPUE	8 (0–146)	0 (0–0)	13 (0–89)			
12	Walleye CPUE	1 (0–15)	2 (0–7)	2 (0–11)			
13	Golden shiner CPUE	1 (0–25)	10 (0–85)	2 (0–18)			

Figure 1. Variations in total zooplankton species richness among reference lakes (open boxes, *n*=20), cut lakes (hatched boxes, *n*=9) and burnt lakes (shaded boxes, *n*=9), by sampling dates and cumulated over the three sampling dates (A). Idem for Rotifera (B), Crustacea (C), and the Shannon diversity index (D). Boxes represent 25th and 75th quantiles. The line across the middle of the box identifies the median. Whiskers extend from the 10th to the 90th quantiles.

Figure 1

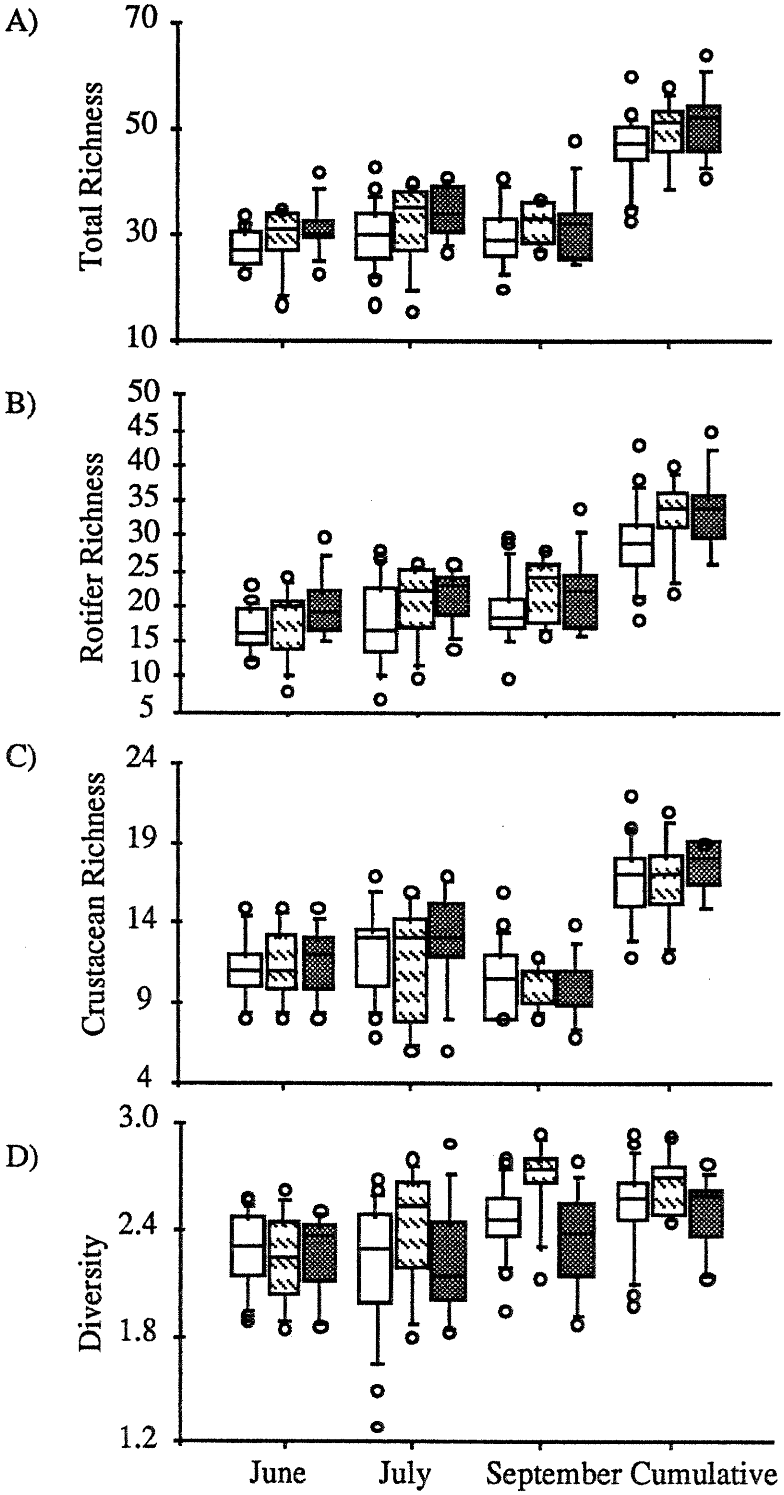

A)
70
50
30
10
Total Richness
B)
50
45
40
35
30
25
20
15
10
5
Rotifer Richness
C)
24
19
14
9
4
Crustacean Richness
D)
3.0
2.4
1.8
1.2
Diversity
June
July
September
Cumulative

Figure 2. Rank-frequency diagrams of rotifers (A) and crustaceans (B) for reference (bars with standard errors), cut (crosses), and burnt (triangles) lakes. Only 21 out of the 41 species of rotifers are represented for clarity. Standard errors in cut and burnt lakes were comparable to those in reference lakes.

Figure 2A)

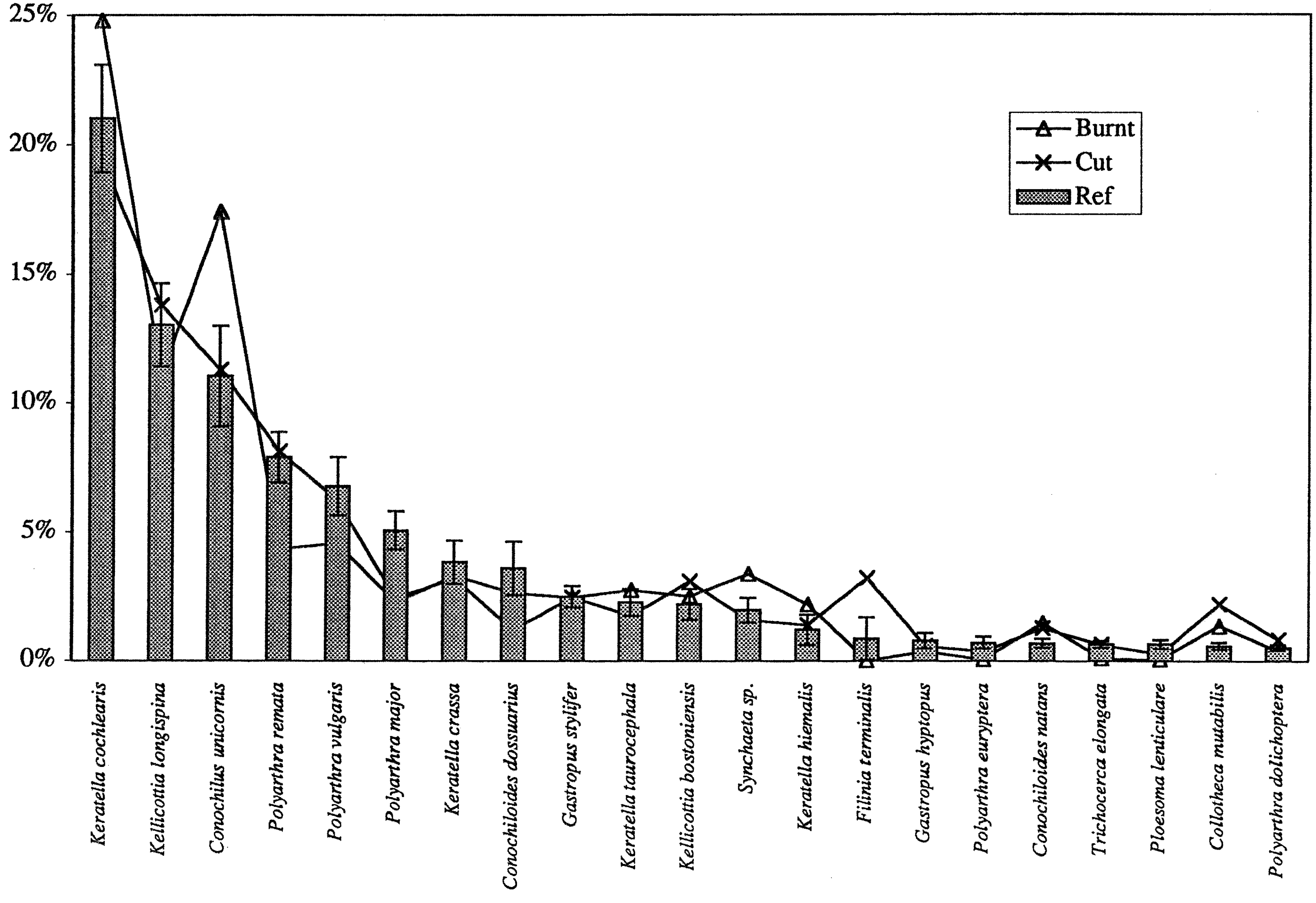

25%
20%
15%
10%
5%
0%
Burnt
Cut
Ref
Keratella cochlearis
Kellicottia longispina
Conochilus unicornis
Polyarthra remata
Polyarthra vulgaris
Polyarthra major
Keratella crassa
Conochiloides dossuarius
Gastropus stylifer
Keratella taurocephala
Kellicottia bostoniensis
Synchaeta sp.
Keratella hiemalis
Filinia terminalis
Gastropus hyptopus
Polyarthra euryptera
Conochiloides natans
Trichocerca elongata
Ploesoma lenticulare
Collotheca mutabilis
Polyarthra dolichoptera

Figure 2B)

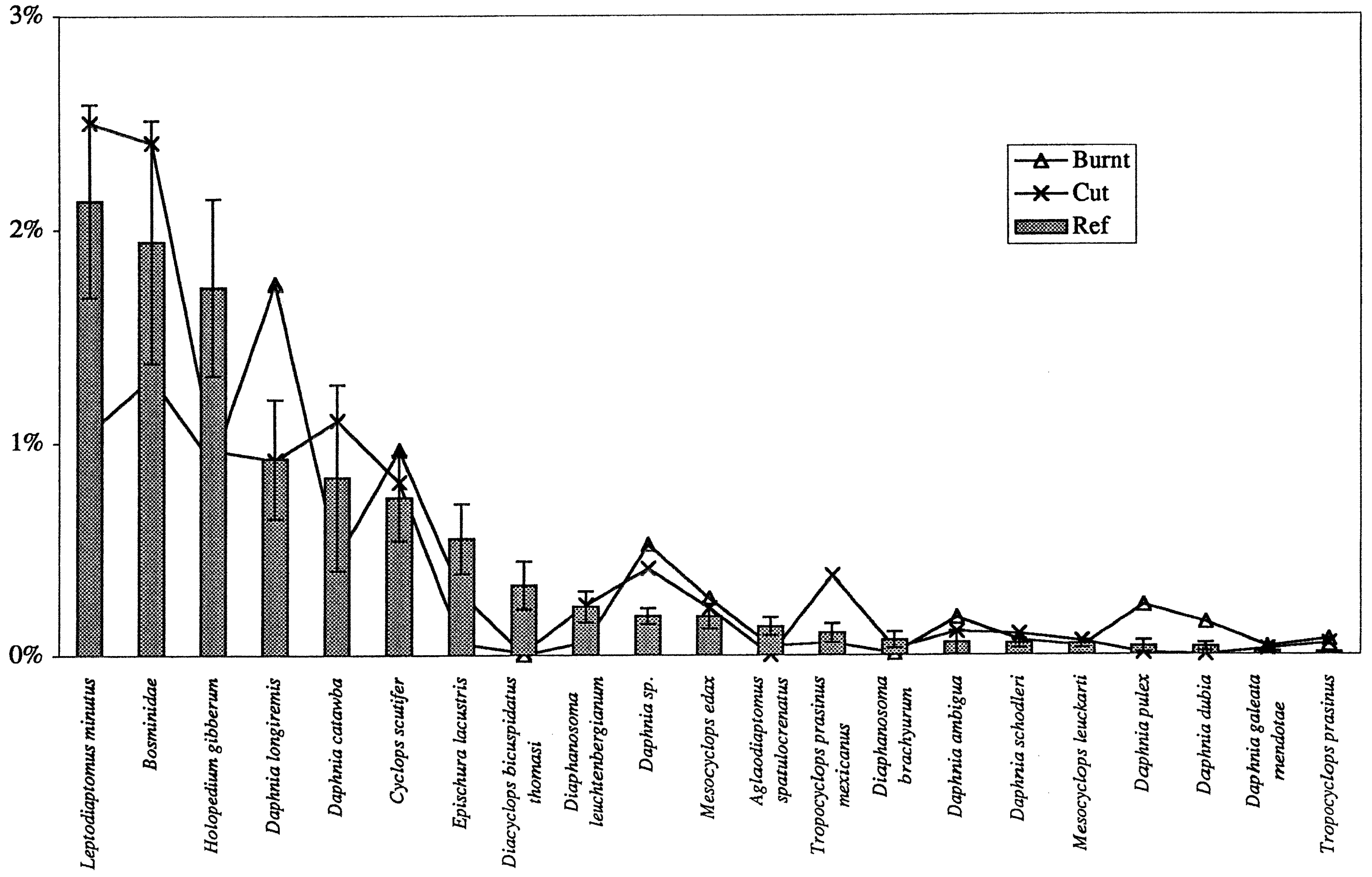

3%
2%
1%
0%
Burnt
Cut
Ref
Leptodiaptomus minutus
Bosminidae
Holopedium gibberum
Daphnia longiremis
Daphnia catawba
Cyclops scutifer
Epischura lacustris
Diacyclops bicuspidatus thomasi
Diaphanosoma leuchtenbergianum
Daphnia sp.
Mesocyclops edax
Aglaodiaptomus spatulocrenatus
Tropocyclops prasinus mexicanus
Diaphanosoma brachyurum
Daphnia ambigua
Daphnia schodleri
Mesocyclops leuckarti
Daphnia pulex
Daphnia dubia
Daphnia galeata mendotae
Tropocyclops prasinus

Figure 3. Canonical correspondence analysis (CCA) ordination plots of zooplankton species assemblages constrained by catchment type (A), and sampling date (B). Ordination of samples (zooplankton communities) are illustrated on the left panel, while the species-environment biplots are illustrated on the right panel. Sample centroids illustrated in biplots represent the average position of samples for each class variable: R for reference lakes, C for cut lakes, B for burnt lakes in A; June, July, and Sept. samples in B. Species vectors are represented by dots instead of arrows for clarity. Percent variance explained by catchment condition is 3.0% (P=0.048); percent variance explained by sampling date is 9.5% (P=0.001 for overall test and axes I and II). Note that the loading of species vectors on canonical axes is greater in B (time-constrained ordination) than in A (catchment type-constrained ordination).

Figure 3

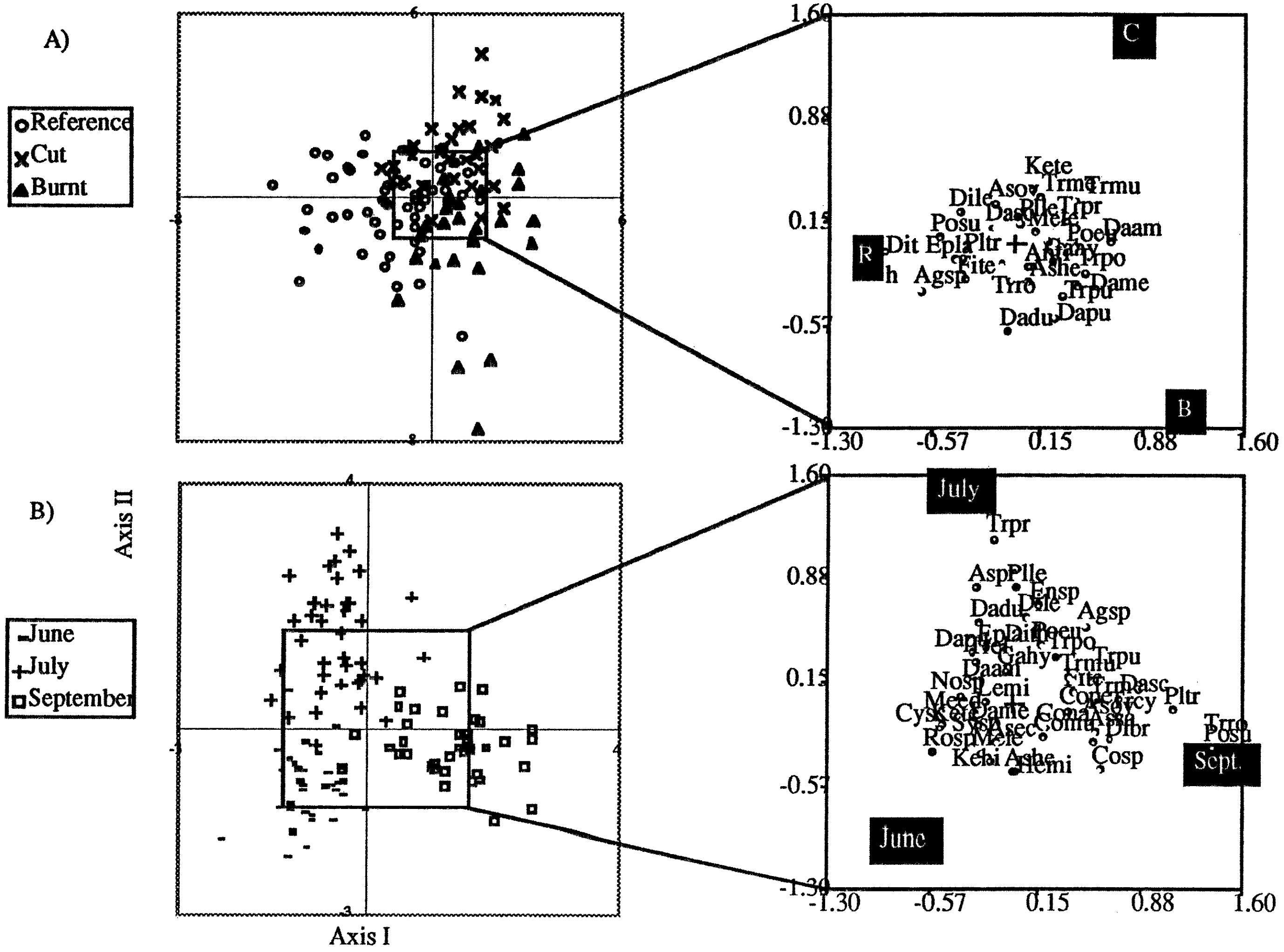

A)
Reference
Cut
Burnt
1.60
0.88
0.15
-0.57
-1.30
-0.57
0.15
0.88
1.60
C
B
R
Kete
Trmu
Dile
Aso
Trpr
Posu
Daam
Dit
Epla
Pltr
Poeu
Trpo
Agsp
Fite
Ashe
Trro
Dame
Trpu
Dadu
Dapu
B)
Axis II
June
July
September
Axis I
July
June
Sept.
Trpr
Asp
Plle
Ensp
Dadu
Dile
Agsp
Trpo
Trpu
Daam
Gahy
Trmu
Dasc
Nosp
Lemi
Pltr
Cosp
Ashe
Trro
Posu

Figure 4. Canonical correspondence analysis ordination plots of zooplankton species assemblages constrained by the 13 selected environmental variables. Ordination plot of the 114 zooplankton communities coded by A) catchment type (open circles for reference lakes, crosses for logged lakes, triangles for burnt lakes) and B) sampling date (bars for June; + for July; squares for September). C) species-environment biplot. Only 7 out of the 13 environmental vectors are illustrated for clarity. Species vectors are represented by dots instead of arrows for clarity.

Figure 4

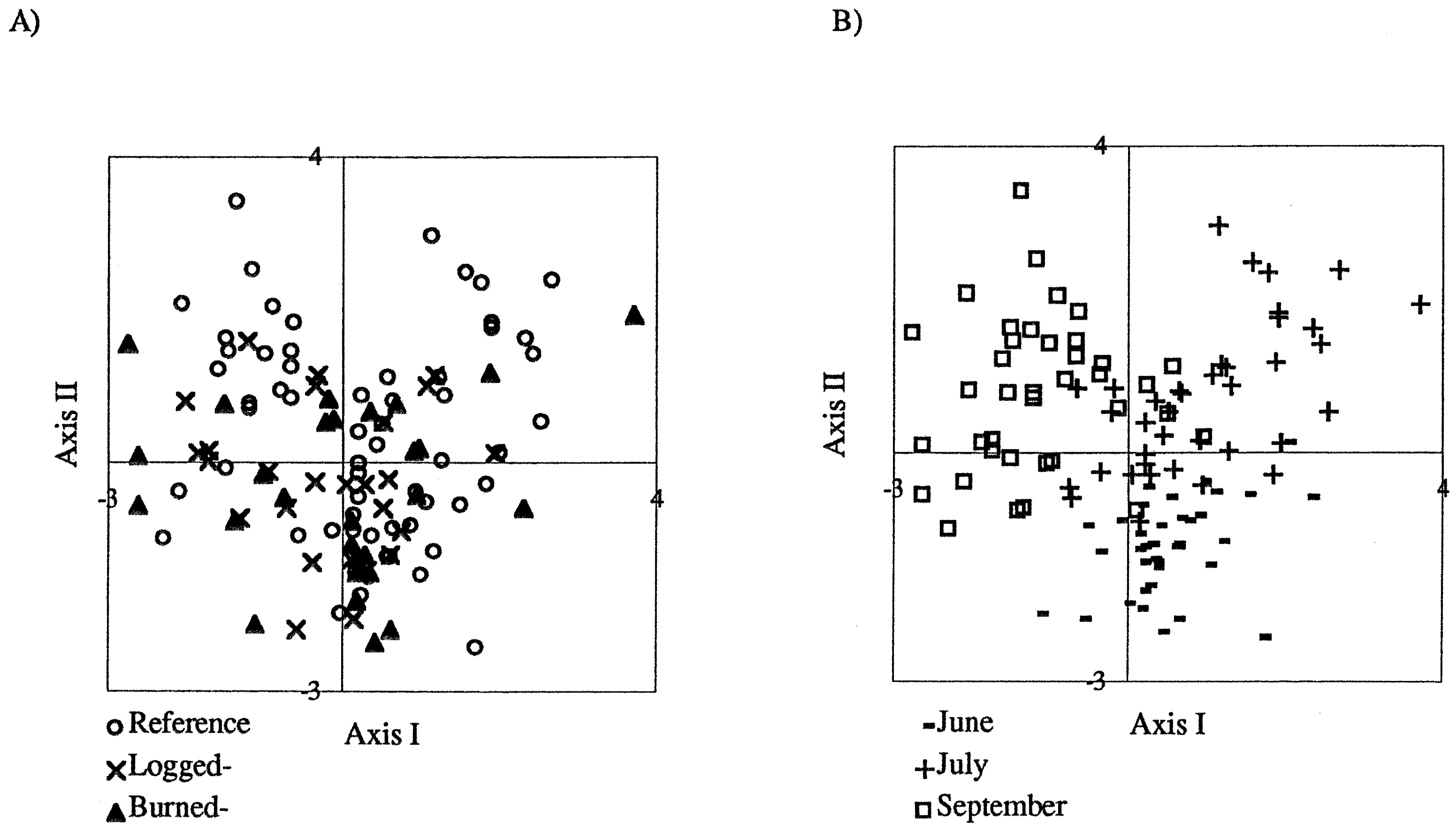

A)
4
-3
4
-3
Axis II
Axis I
Reference
Logged-
Burned-
B)
4
-3
4
-3
Axis II
Axis I
-June
+July
September

Figure 4C)

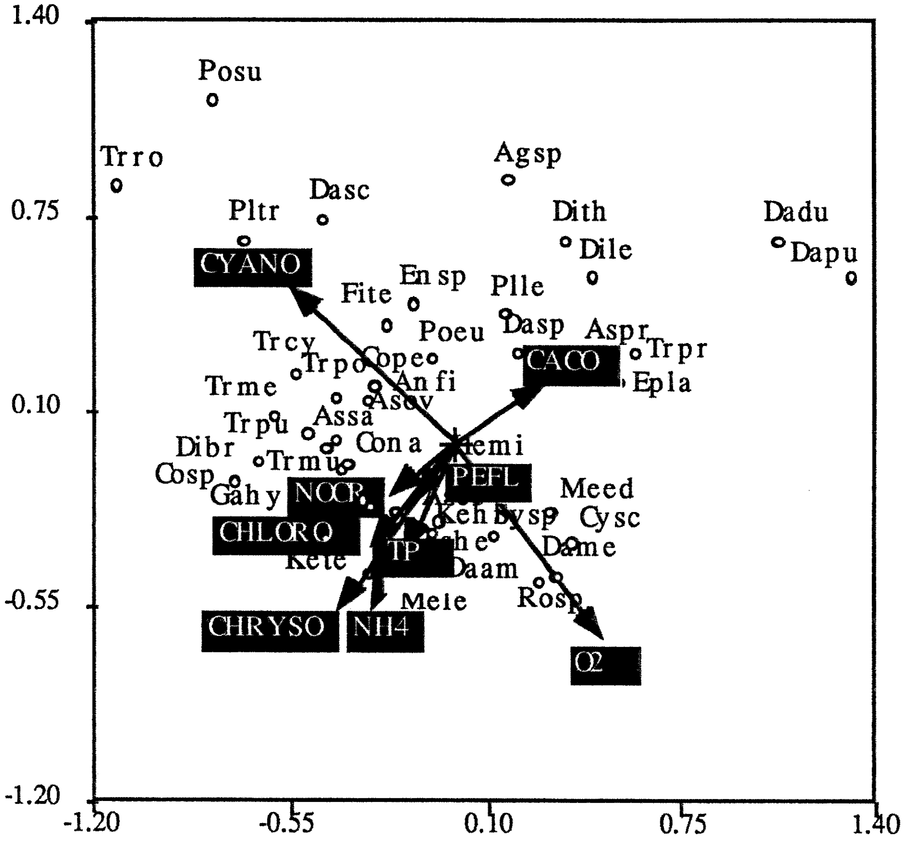
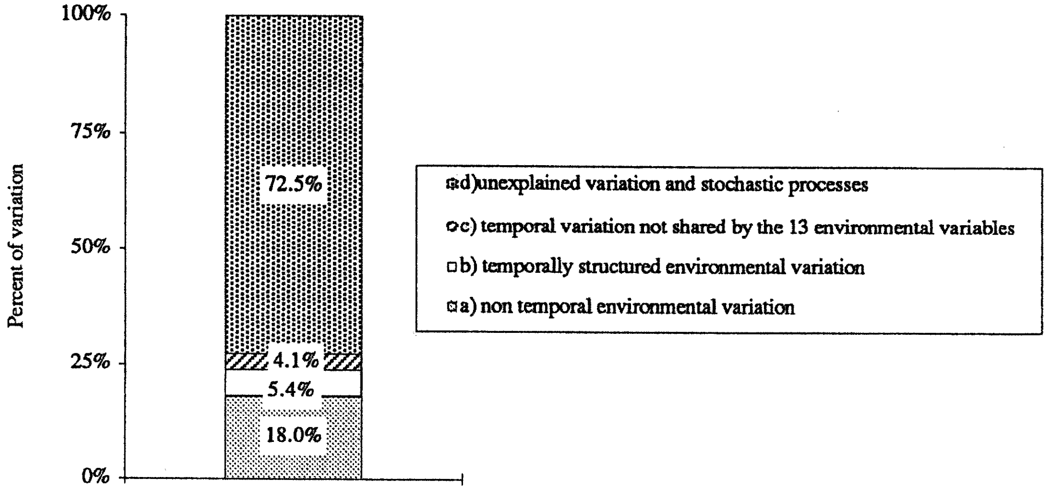
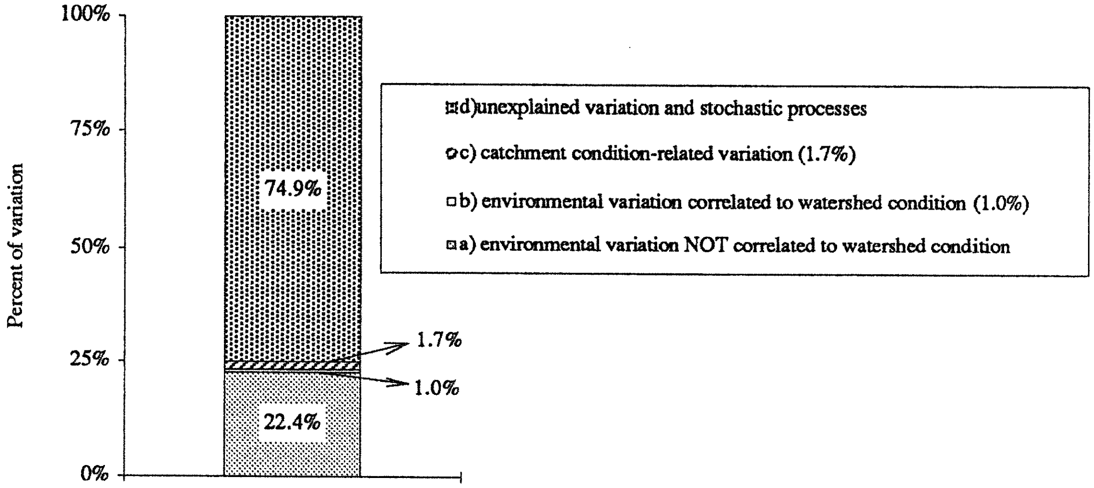

1.40
0.75
0.10
-0.55
-1.20
-1.20
-0.55
0.10
0.75
1.40
Posu
Trro
Agsp
Dasc
Pltr
Dith
Dadu
Dile
Dapu
CYANO
Ensp
Fite
Plle
Poeu
Dasp
Aspr
Trpr
Trcy
Trpo
Cope
CACO
Epla
Anfi
Trme
Asov
Assa
Trpu
Cona
Hemi
Dibr
Trmu
Cosp
PEFL
Meed
Gahy
NOCR
Kehi
Sysp
Cysc
CHLORO
Kehe
Dame
Kete
TP
Daam
Rosp
Mele
CHRYSO
NH4
O2

Figure 5. Variance partitioning of the zooplankton species matrix between the selected 13 environmental factors and A) sampling date; B) catchment condition.

A)



B)



CHAPITRE III - Influence of catchment deforestation by logging and natural forest fires on crustacean community size structure in lakes of the Eastern Boreal Canadian forest

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[redacted]

Abstract

Logging and wildfires are important perturbation factors of the Canadian boreal forest, but their effects on aquatic communities remain largely unknown. Here, we use zooplankton community size structure to assess the ecological effects of logging and wildfires on aquatic communities.

The lab version of the optical particle counter was used to establish the crustacean size spectra of zooplankton samples collected in 38 lakes characterized by different catchment conditions: logged in 1995 (nine "logged" lakes); burnt in 1995 (nine "burnt" lakes); left unperturbed since the past 70 years (20 reference lakes). Size spectra present crustacean biovolume in 22 size classes, from 200-300 μm equivalent spherical diameter (ESD) to 2300-2400 μm ESD.

The among-group variation in size spectra was significant one and two years following catchment perturbations. Size spectra in logged and burnt lakes were on average shifted towards larger size classes relative to reference lakes, although the reference and burnt groups of lakes represented the only pair significantly different from one another. As a result, biovolume of crustacean particles > 1100 μm ESD in burnt lakes was on average higher by 360% relative to reference lakes.

Among a set of 15 water quality variables and 14 fish species density variables, potassium concentration and white sucker density were the most important environmental correlates of crustacean size structure. Despite important lake- and month-specific variations within each group of lakes, the size-based approach was successful in showing an effect that could be common to both logging and forest fires, namely a shift towards larger crustacean organisms.

Introduction

Logging and natural forest fires are common disturbances of the Canadian boreal forest (Canadian Forest Service, 1998). Though logging and forest fires can alter stream water chemistry and biota, little is known about their respective effects on lacustrine ecosystems. Effects of logging on lake ecology can include increases in primary productivity (Rask *et al.*, 1993) and decreases in brook trout density (Bérubé and Lévesque, 1998). Since zooplanktonic organisms rely on primary producers as a food source, and serve in turn as a food source for fish, zooplankton community structure may also be expected to be affected by logging. The density of cladocerans and copepods, however, appears to be relatively unaffected by logging when less than 35% of the catchment surface area has been clear-cut (Rask *et al.*, 1998). A more recent study compared the effects of logging and forest fires on the biomass of different zooplankton taxonomic groups, and different zooplankton size fractions (Patoine *et al.*, 2000). In this study, the biomass of cladocerans and cyclopoids were not affected by logging or forest fires, but the biomass of calanoids was slightly depressed in logged lakes. In contrast, among-group differences in zooplankton biomass were better resolved when divided into different size fractions. The biomass of the 100-200 µm size fraction (predominantly algae, rotifers, and nauplii) was higher in burnt lakes than in reference lakes during the first and second year after perturbations, as was the > 500 µm (adult stages of crustaceans) size fraction during the second year. This suggests that a size-based approach to zooplankton community structure might be better adapted to monitor changes associated with catchment perturbations than a taxon-based approach. In fact, the size structure of zooplankton communities has previously been shown to correlate as well, or slightly better, to lake morphometry and water quality than could taxonomic structure (Sprules and Holtby, 1979). In addition zooplankton community size structure can be sensitive to various environmental perturbations such as eutrophication (Sprules and Munawar, 1986), recreational access to lakes (Harig and Bain, 1998), acidification (Schindler, 1990), and chemical contamination (Havens and Hanazato, 1993). It has been hypothesized that environmental perturbations can be accompanied by a shift in community size structure from large to small organisms (Odum, 1969). Indeed, he proposed that the smaller individuals of a community, by virtue of their short generation time relative to larger organisms, have a greater ability to colonize and dominate newly created or changing environments such as those under stress. Whether logging and forest fires represent perturbation factors characterized by a shift in zooplankton community size structure remains unknown.

The size structure of zooplankton communities, however, is not only influenced by environmental perturbations. Among-lake variations in zooplankton community size structure has been attributed to differences in vertebrate predation pressure, and led to the formulation of the size efficiency hypothesis (Brooks and Dodson, 1965). According to this hypothesis, the size structure of zooplankton communities shifts towards smaller sizes in the presence of planktivorous fish, as planktivorous fish preferentially feed on the larger-sized zooplankton individuals. Indeed, recent evidence suggests that the biomass of macro-zooplankton (variously defined as adult stages of crustaceans, Cladocera > 1 mm, or plankton > 75 μm) is more strongly correlated (negatively) with fish density data than with nutrient concentration data. Inversely, micro-zooplankton is more strongly correlated (positively) with nutrient concentration than with fish density (McQueen *et al.*, 1986; Quiros, 1991). Zooplankton community size structure may thus reflect processes related to both nutrient enrichment (bottom-up processes) and fish predation intensity (top-down processes). Since one of the most widely reported effects of logging activities and wildfires on stream chemistry is an increase in nutrient concentration (Jewett *et al.*, 1995; Likens *et al.*, 1970; Nicolson, 1975; Schindler *et al.*, 1980; Wright, 1976), we might expect zooplankton community structure in cut and burnt lakes to be shifted towards smaller-sized organisms.

One of the projects being pursued by the Sustainable Forest Management Network (Adamowicz, 1999) aims at comparing the effects of disturbances by logging and forest fires on lake chemistry and biota (Carignan *et al.*, 2000). Three groups of lakes differing in their catchment conditions (unperturbed, logged in 1995, or burnt in 1995) have been investigated since 1996. The concentration of total phosphorus (TP) was significantly higher in logged and burnt lakes relative to reference lakes during the three years following catchment perturbations (Carignan *et al.*, 2000).

Here, we used the optical particle counter (Herman, 1988) to determine the size structure of the crustacean communities of the same sets of lakes, one and two years after logging and fires. The goal of this study is to test whether wildfires or industrial logging represent a significant source of variation in crustacean community size structure. Since TP was generally higher in "logged lakes" and "burnt lakes" relative to reference lakes (Table 1), we expected the zooplankton community size structure in the former lakes to be shifted towards smaller-sized zooplankton organisms relative to reference lakes. Among-lake variations in size spectra were also examined in relation to bottom-up and top-down variables. We expected nutrients, particularly TP, to be an important, positive correlate of smaller size classes, and fish density to correlate negatively with larger size classes.

Material and Methods

STUDY AREA

The lakes were located within a 30 000 km^2 area, in Eastern Canada. Details on catchment physiography, lake morphometry and water chemistry are presented in Carignan *et al.* (2000). Briefly, the three groups of lakes shared similar mean depths, lake areas, drainage ratios (ratio of catchment area over lake area), and pH values (Table 1). Logged catchment (n=9) were clear-cut in 1995 on 9% to 73% of their surface areas; 20-m buffer zones of unharvested vegetation were left around their lakes. Burnt catchment (n=9) had nearly 100% of their area burnt by wildfires in 1995, except for one catchment that was only burnt on 50% of its surface. The reference group of lakes have had unperturbed catchments for the past 70 year. It was composed of 20 lakes in 1996, during the first year of sampling. Four of these lakes had their catchment partially clear-cut after the first sampling season; these were not considered in the analyses of 1997 data presented here.

The 38 lakes were sampled within one week during the months of June, July, September 1996 (one year after catchment perturbations) and 1997 (two years after catchment perturbations). Zooplankton samples were collected at the deepest point of the lake with a cantilevering net (Filion *et al.*, 1993) fitted with 53 µm mesh size net, from 1 m above the sediments to the surface. Three replicate samples per lake were collected at the same station. The samples were preserved by addition of carbonated water followed by addition of formaldehyde to a final concentration of 4% vol/vol. Samples for chemical analyses and phytoplankton enumeration were collected from the euphotic zone (1% of incident PAR) with an integrated tube (Carignan *et al.*, 2000; Planas *et al.*, 2000). Fish sampling in the 38 lakes was performed over two years (1996, 1997) using experimental monofilament gillnets with a fishing effort of between 6 and 12 nets per lake per night, depending on lake area (St-Onge and Magnan, 2000).

LABORATORY ANALYSES

Zooplankton samples were examined under a dissecting microscope to remove *Chaoborus* larvae. Each replicate sample was divided with a Folsom splitter into two halves, one of which was subsequently divided further to give us three fractions of the original sample (1/2, 1/4, 1/4). Zooplankton analyses with the Optical Plankton Counter were performed on one of the smaller fractions (the other fractions were kept for taxonomic analyses and dry weight determinations).

The lab version of the Optical Plankton Counter (OPC-1L) (Focal Technologies, 1992) was used to determine crustacean size spectra as described in Herman (1988) with the following adaptations: pump flow was 9 $l\cdot min^{-1}$ for a linear flow of 0.5 $m\cdot s^{-1}$. Water circulated through a closed circuit composed of an aquarium in which the zooplankton samples were kept in suspension, a pump, the detector and a 53 µm mesh bucket inserted in the aquarium. Counts never exceeded 40 particles•sec^{-1}. Counts were grouped in 100 µm equivalent spherical diameter (ESD) size classes and transformed into biovolume by using the geometric formula for the volume of a sphere (volume=$\pi(\text{ESD})^3/6$). Size spectra representing biovolume on the Y axis (mm^3 of crustacean particles per m^3 of water, log(x+1)) and size class on the X axis (200 to 3000 µm ESD) were constructed for each of the 228 samples representing the 38 lakes sampled three times per year during two consecutive years. Size classes occurring in 5% or less of the lakes were eliminated. As a result, size spectra presented 22 size classes, from 200-300 µm to 2300-2400 µm ESD. Because of their small size, rotifers are undetected by the OPC. Results therefore pertain uniquely to the crustacean community.

STATISTICAL ANALYSES

Description of size spectra

The entire data set was composed of 228 samples (rows, representing the 38 lakes sampled three times per year during two years) and 22 descriptors (columns, representing 22 size classes). Principal component analysis (PCA) was used to describe the overall variability in the 228 size spectra, and to identify what size classes, among the 22, show the greatest amount of variance (Legendre and Legendre, 1998: 391). PCA was performed with the R statistical package (Casgrain and Legendre, 2000) on the covariance matrix, with eigenvectors normalised to unity.

Influence of catchment condition on size spectra

Redundancy analysis (RDA) was used to test the hypothesis that catchment condition is a significant source of variation in crustacean size spectra, one, and two years after catchment disturbances. During an RDA, a dependent or “species” matrix (here size spectra) is related to an “environmental” matrix (here catchment condition) by assuming linear relationships between matrices (ter Braak and Prentice, 1988). Analyses were performed on the 1996 average size spectra (20 reference lakes, 9 cut lakes, 9 burnt lakes), and on the 1997 average size spectra (16 reference lakes, 9 cut lakes, 9 burnt lakes). Annual average size spectra were computed for 1996, and for 1997, by taking, for each size class, the average log(x+1)-transformed biovolume value of the three sampling periods (June, July, September). The dependent matrix thus consisted of 38 rows representing the 38 lakes, and 22 columns, representing the 22 size classes. The "environmental matrix" consisted of 38 rows and three columns of binary data coding for catchment type. The analysis is thus analogous to a multivariate analysis of variance, with the added advantage that there is no upper limit to the number of species that can be analysed. Analyses were performed on the covariance matrix with eigenvectors normalized to 1 to obtain distance biplots, as suggested by Legendre and Legendre (1998: 589) in cases involving class variables in the environmental matrix. Significance testing was performed by 999 random, unrestricted row permutations. If catchment condition was declared a significant source of variation of size spectra (α=5%), three additional RDAs were performed to determine which pairs represented different groups. RDAs were performed with the Canoco program version 3.11 developed by ter Braak (1990).

Influence of catchment condition on crustacean biovolume

Biovolumes in two coarse-scale regions of the size spectrum were calculated. The "small" crustacean fraction corresponded to the sum of biovolumes in size classes 200-1100 μm. The "large" crustacean fraction corresponded to the sum of biovolumes in size classes 1100-2400 μm. The 1100 μm cut-off point was established due to the existence of a trough in this region of many size spectra (cf. Results). Total biovolume will refer to the sum of biovolumes in all size classes. Last, community mean size was calculated as the mean of the biovolume distribution among the 22 size class, and is expressed in μm ESD.

Among-group differences in total biovolume, "small" crustacean biovolume, "large" crustacean biovolume, and mean size were examined separately for 1996 and 1997 with one-way, repeated-measure, mixed-model ANOVAs (RM-ANOVAs) (Sokal and Rohlf, 1981: 284). Catchment condition was treated as the main, fixed factor with three levels (reference, logged, burnt). Lakes constituted the first nested factor with 38 random levels (34 in 1997) unequally distributed among the three fixed factors: 20 in the reference group (16 in 1997), nine in the logged group, nine in the burnt group. The mean square associated with the lake factor served as the *F*-statistic denominator for the hypothesis that catchment condition was a significant source of variation. The repeated sampling of lakes was treated as a second nested factor with three random levels equally distributed among the lakes: June, July, and September. Variance components for the lake and month factors could thus be isolated for each variable (small, large, and total biovolume, mean size). Because the month factor was the most important source of variation, separate ANOVAs were also performed for each sampling date separately. Biovolume data were skewed to the right; they were $\log_{10}(x+1)$ transformed prior to analyses to satisfy the normality condition of ANOVAs. Mean size data were left untransformed. In the cases where the *F* statistic was significant ($\alpha=5\%$), comparisons of individual means were performed with the Tukey-Kramer Honestly Significant Difference test. Homoscedasticity of data was tested with Levene's test. ANOVAs were performed with Jump 3 (SAS Institute, 1994).

Influence of perturbation intensity on crustacean biovolume

Lake concentration of TP and various ions were positively correlated with ratios of deforested area (by logging or burning) over lake volume ("volumetric impact ratio", or "VIR") (Carignan *et al.*, 2000). Here, we used simple linear regression analyses to test if crustacean biovolume in the small and large size fractions (dependent variable) was similarly related to VIR, the ratio of deforested area over catchment area ("%DEF"), or a modified version of VIR (VIR': deforested area/lake volume + catchment area/lake volume). VIR' takes into account the effect of total catchment area in addition to that related to deforestation. Regression analyses were performed on average 1996 data sets (mean of June, July, and September values) of logged lakes alone, burnt lakes alone, or logged and burnt lakes pooled together. Biovolume data were $\log_{10}(x+1)$ transformed. Regression analyses were performed with Jump 3 (SAS Institute, 1994).

Influence of bottom-up and top-down variables on size spectra

Relationships between crustacean size spectra and the environmental variables listed in Table 2 were examined by an RDA performed on two-year average data. Average size spectra were computed by taking the average of the six log(x+1)-transformed biovolume values corresponding to the six sampling events over two years. In this case, the environmental matrix consisted of 38 rows (lakes) and 29 columns representing the 29 environmental variables listed in Table 2. These environmental variables were assigned to two sets: bottom-up (15 variables) or top-down (14 variables). Bottom-up variables included those that characterized the fluid environment on which zooplankton rely to feed. Top-down variables included the density of potential invertebrate (*Chaobrous* larvae) and vertebrate predators of zooplankton. One RDA was performed for each environmental variable. The percent of variance in the dependent matrix that could statistically be explained by each environmental variable was tested for significance ($\alpha=0.05$) by 999 unrestricted random permutations of residuals ("full" model). A forward selection procedure was then applied to the entire set of 29 variables to obtain a small subset of environmental variables that explained a maximum of variability in size-spectra. Significance testing ($\alpha=0.05$) was performed at each selection step with 999 unrestricted permutations under a full model. Analyses were performed so as to obtain correlation biplot, and data were centered and standardized by size classes.

Two-year averages were computed for RDA analyses of size spectra with bottom-up and top-down variables because the inter-annual variability in size spectra was low, as suggested by the similarity of results between the 1996 and 1997 RDAs of size spectra with catchment condition (cf. Results, p. 114). Furthermore, preliminary analyses showed that the same environmental variables were selected when separate RDAs were performed for the 1996 data set and the 1997 data set.

Results

DESCRIPTION OF SIZE SPECTRA

Differences among the 228 size spectra were mostly the result of biovolume variations in size classes 1200-1500 μm, as indicated by the high loading of these size class vectors on the first principal component axis (Figure 1A). This first axis accounted for 58% of the total variance among the 228 samples. Axis II accounted for 16% of total variance, and represented mostly variation in size classes 800-1100 μm (positive loading on axis II), and 1600-1800 μm (negative loadings on axis II) (Figure 1A). Axis III accounted for only 8% of total variance, and represented variation in size classes 1700-1900 μm (not shown). Variation in size classes 200-700 μm did not contribute significantly to axes I or II, meaning that all size spectra had invariant biovolume in small size classes relative to larger size classes. The first two axes could therefore capture 74% of the variation among the 228 samples representing the 38 lakes sampled six times over two consecutive summers. Samples from burnt lakes generally ranked higher along PCA axis I (mean and standard deviation: +0.9±2.0) than reference samples (–0.5±0.9) despite extensive overlap between the two groups (Figure 1B). This suggests zooplankton biovolume in size classes 1200-1500 μm was higher in burnt-catchment lakes than in reference lakes (see hereafter).

Sample points lying close to the origin of PCA axes I and II (Figure 1B) represent "average" size spectra. One such example is illustrated in Figure 2: lake C24 sampled in September 1996 (coded C24c) has a continuous distribution of crustacean particles in classes 200-300 μm to 1300-1400 μm with, in each class, biovolumes varying between 10 and 50 $mm^3 \cdot m^{-3}$ (values back-transformed from log(x+1)=1 and log(x+1)=1.7). From the negative end of PCA axis I to the positive end, we expect maximum increases of biovolume in size classes 1200-1500 μm (Figure 1A). This is illustrated in Figure 2 by samples P110 September 1997 (P110f, negative end of axis I) and FBP10 June 1997

(FBP10d, positive end of axis I). In the former sample (P110f), no crustacean particles were recorded in size classes 1200-1500 µm (Figure 2). In the latter sample (FBP10d), on the contrary, biovolume in size classes 1200-1500 µm varied between 100 and 315 $mm^3 \cdot m^{-3}$ (Figure 2).

PCA axis II separated unimodal distributions (positive end of axis II) from bimodal distributions (negative end of axis II). Sample FBP9 June 1997 (FBP9d) is a good example of a bimodal distribution: biovolume in size classes 900-1100 µm was zero, and more than 10 $mm^3 \cdot m^{-3}$ in the larger size class 1700-1800 µm. The other size spectra in Figure 2 illustrate the breadth of variation in the range of crustacean particle size encountered, in the biovolume of each size class, and in the overall shape of the size spectra.

INFLUENCE OF CATCHMENT CONDITION ON SIZE SPECTRA

Catchment condition was a significant source of variation in crustacean size spectra one (P=0.029) and two (P=0.019) years after catchment disturbances (Table 3). One year after disturbances (1996), the first canonical axis accounted for 12.5% of size spectra variations (P=0.027), and contrasted reference lakes to burnt lakes (Figure 3A). Projections of the burnt-lakes centroid and the reference lakes centroid at right angle on vectors of the 1100-1500 µm size classes show that burnt lakes, as a group, had higher biovolume values in these size classes than reference lakes. The second canonical axis contrasted logged lakes against reference and burnt lakes, but was not significant (P=0.77), suggesting size spectra of logged lakes were not significantly different from either reference or burnt lakes. Pairwise comparisons of the three groups of lakes confirmed this to some degree: the difference between reference and burnt lakes was indeed the only one significant at the 5% level (P=0.021, Table 3). The difference between reference and logged lakes, (P=0.081), and that between logged and burnt lakes (P=0.58) were not significant (Table

3). Despite a great deal of within group-variation, differences in size spectra between burnt and reference lakes can be seen as an increase in the biovolume of all size classes, but particularly so of the 1100-1500 μm size classes (Figure 4). The average size spectra of logged lakes was intermediate between those of reference and burnt lakes. Two years following perturbations (1997), catchment condition remained a significant source of among-group variation in zooplankton size spectra, and accounted for roughly the same amount of variance (14.5%, P=0.019, Table 3). Pairwise comparisons revealed that, on average, size spectra in burnt lakes differed from those in reference lakes (P=0.008), while those in logged lakes did not differ significantly form those of reference (P=0.25) or burnt lakes (P=0.21) (Table 3). The lake ordination in 1997 was similar to that in 1996, and is therefore not presented here.

INFLUENCE OF CATCHMENT CONDITION ON CRUSTACEAN BIOVOLUME

The previous mutlivariate approach to size spectra analysis allowed us to identify what range of size classes seems sensitive to catchment disturbances (1100-1500 μm). It also allowed us to identify the region of 900-1100 μm as either characterizing the largest size class recorded in many samples, or as a trough in bimodal size spectra. It thus seemed natural to use the 900-1100 μm as a cut-off point to create two crustacean size fractions: a "small" one represented by the sum of the biovolumes in size classes 200-1100 μm, and a "large" one represented by the sum of the biovolume in size classes 1100-2400 μm. Total biovolume represented the sum of biovolumes over the entire 22 size classes.

Total biovolume did not differ significantly among the three groups of lakes during the first, nor during the second year after catchment perturbations (Table 4, Figure 5C). The small crustacean fraction represented on average 81% of total biovolume, with a range encompassing 16% to 100%. There were no significant among-group differences in small crustacean biovolume in 1996, nor in 1997 (Table 4, Figure 5A). Biovolume of large crustaceans, however, was significantly higher in burnt lakes than in reference lakes in both 1996 (*P*=0.022) and 1997 (*P*=0.032) by 366% and 388% respectively (based on back-transformed means) (Table 4, Figure 5B). In logged lakes, biovolume of large crustaceans was on average higher by 240% relative to reference lakes one year after logging, but this difference could not be declared significant (*P*=0.060). Two years following logging, this biovolume difference decreased to 172% and was not significant (*P*=0.15). As a consequence of higher biovolume values in the larger size fraction of crustaceans in perturbed-catchment lakes, community mean size was on average higher by ca. 20% in both logged and burnt lakes relative to reference lakes (652 μm) one year after perturbations, though the variation was not significant (*P*=0.058, Table 4, Figure 5D). Two years after perturbations, the among-group variation in community mean size was significant (*P*=0.042), with values in burnt lakes 20% higher than in reference lakes (Table 4, Figure 5D).

The nested design of the previous ANOVAs allowed us to isolate the month and lake variance components of small, large, and total biovolume, and mean size. With more than 60% of total variance, the month factor was clearly the most important source of variation for all variables, both one and two years following catchment perturbations (Table 4). Mixed-model ANOVAs such as those used here do not formally allow for the calculation of a variance component for the main, fixed treatment factor. If one supposes, for a moment, pure model II models (where the main treatment factor - here catchment condition - is treated as a random variable i.e. whose value is unknown before measurement), one obtains catchment condition variance components smaller than 13% for the four variables examined, during both years.

Because month was such an important source of variation (Table 4), we examined among-group differences for each month separately (Figure 6). Analyses of variance based on monthly data did not result in the detection of among-group differences that had not previously been detected by the repeated measure ANOVAs. Significant among-group differences were detected only in the case of large crustacean biovolume, during the June sampling round, when values in burnt lakes were 600% higher than those in reference lakes (P=0.017). Among-group differences in July and September were non-significant (P=0.11 and 0.28 respectively). Seasonal variation in the three groups of lakes was similar, with greatest biovolume generally achieved during the month of July of both years.

INFLUENCE OF PERTURBATION INTENSITY ON CRUSTACEAN BIOVOLUME

The biovolume of large crustaceans could not be predicted from perturbation intensity (P>0.3), whether the latter was expressed as VIR, %DEF, or VIR', and no matter what subset of lakes was used (logged alone, burnt alone, logged and burnt pooled). The biovolume of small crustaceans, however, could be predicted from %DEF when logged and burnt lakes were pooled together (r^2=23%, P=0.042, Figure 7). The little overlap in the ranges of disturbance intensity between the logged and burnt groups of lakes precludes the use of a single regresssion equation to model the relationship between the biovolume of small crustaceans and disturbance intensity for both groups of lakes. The regression equation for the logged group of lakes had an r^2 of 40% and a probability value of 0.066. This contrasts with the highly significant r^2 of 77% (P=0.002) reported in Patoine *et al.* (2000) for the same set of lakes between %DEF and the biomass of limnoplankton in the 100-200 μm size class (mostly rotifers, nauplii and algae, particles mostly undetected by the OPC). It thus seems that the biomass of the smaller planktonic organisms are more sensitive to catchment logging than larger ones (those comprised between 200 and 1000 μm ESD). Because the probability value of 0.066 is close to the level of 0.05 fixed for statistical significance, it may be worth considering what would be the implications of a true positive relationship between the biovolume of small crustacean and logging intensity (here gone undetected because of insufficient statistical power). A positive relationship between %DEF and the biovolume of small crustacean in logged lakes suggests there could be a biovolume increase of small crustacean in logged lakes relative to reference lakes if one considered a group of logged lakes that excluded catchments with low proportions of logging. Such an interpretation is consistent with results by Rask *et al.* (1998) who could not show any significant effect of logging on crustacean density in lakes with less than 35% of the catchment area logged. In our set of lakes, three out of nine lakes had less than 35% of their catchment area logged, and only three had more than 50%. Overall, the extent of logging may have been on average too low for the biovolume of small crustaceans to increase relative to reference lakes, as it did for the biomass of rotifers, nauplii and algae (Patoine *et al.*, 2000).

INFLUENCE OF BOTTOM-UP AND TOP-DOWN VARIABLES ON SIZE SPECTRA

Five variables were selected by the forward selection as significant environmental gradients related to linear variations in size spectra: potassium concentration, phosphorus concentration, white sucker density, brook trout density, and dissolved organic carbon (DOC). Together, these accounted for 42% of the variability in size spectra (P=0.001). Their influence on the biovolume of different size classes is illustrated in Figure 8. Near 0°-angles between environmental vectors and size class vectors indicate positive correlations between environmental variables and biovolume in specific size classes; flat angles indicate negative correlations, while near 90°-angles indicate uncorrelated, independent variables. Canonical axis I represented mostly inverse gradients of potassium concentration and white sucker density; it accounted for 25% of size spectra variability (P=0.001). Axis II represented mostly a TP gradient, and accounted for 13% of size spectra variability (P=0.002). Potassium concentration, phosphorus concentration, and brook trout density were positively correlated to biovolume in all size classes, though the smaller size classes (< 1100 µm ESD) were more tightly correlated to phosphorus, while the larger size classes were more tightly correlated to potassium. Note that the strong link between potassium and size spectra variations, especially in large size classes was coincident with i) potassium concentration in burnt lakes more than three times as elevated as that in reference lakes (Table 1), and ii) biovolume of large size-class crustaceans significantly higher in burnt lakes than in reference lakes (Figure 5B). In comparison, the link between TP and size spectra variations, especially in small size classes, was weaker than that of potassium. Although TP concentration in burnt lakes was higher than in reference lakes, the increase was less than two-fold (Table 1). Consistently, the biovolume of small crustaceans was not significantly higher in burnt lakes than in reference lakes.

The influence of white sucker density shifted from negative in the case of large crustacean biovolume to positive in the case of small crustaceans. White sucker was captured in 31 out of the 38 lakes, making it the most frequently encountered fish species. The relative density of small white sucker individuals (<160 mm) was significantly lower in impacted lakes (logged and burnt) than in reference lakes (St-Onge and Magnan, 2000). The diet of white sucker, however, was composed of less than 1% of zooplankton by dry mass (n=1023, P. Magnan, Université du Québec à Trois-Rivières, Trois-Rivières, Canada, personal communication). In contrast, yellow perch, present in 25 of the 38 lakes, relied on zooplankton for 25% of their diet, and represented on average 35% of the total density of typical planktivorous fish (P. Magnan, Université du Québec à Trois-Rivières, Trois-Rivières, Canada, personal communication). As an environmental variable, however, yellow perch was not a significant environmental variable of size spectra variations (P=0.77, Table 2).

Discussion

Catchment deforestation by logging or wildfires was here associated with a shift in zooplankton size structure towards larger organisms. This contrasts with other types of environmental perturbations generally characterized by a size shift towards smaller zooplankton organisms, namely eutrophication (Sprules and Munawar, 1986), recreational access to lakes (Harig and Bain, 1998), acidification (Schindler, 1990), and chemical contamination (Havens and Hanazato, 1993). Our main hypothesis stating that zooplankton community size structure in logged and burnt lakes should be shifted towards smaller organisms relative to reference lakes, partly based on those previous studies and on theoretical considerations developed in Odum (1985), was thus refuted. Our secondary hypotheses regarding relationships between different size classes and trophic variables, namely that small size classes should be positively correlated to TP, and large size classes negatively correlated to fish density, were supported by our results. These relationships may provide some explanations for the observed size shift towards larger organisms in burnt lakes relative to reference lakes.

First, the influence of TP on small size classes was overridden by the influence of potassium on larger size classes. Since TP increases in logged and burnt lakes relative to reference lakes were not as great as those for potassium, it follows that the size shift in logged and burnt lakes was towards larger-sized rather than smaller-sized crustaceans. The role of potassium as a positive correlate of crustacean biovolume, and especially of the larger size fraction, is unclear. Since potassium concentration was highly correlated to the amount of forest cover loss (Carignan *et al.*, 2000), it could represent changes occurring in several water quality parameters that, together, have direct or indirect (through the phytoplankton community structure) effects on zooplankton community structure. For example, calcium was significantly higher in burnt lakes (average of 2.2 $mg \cdot L^{-1}$) relative to reference lakes (1.5 $mg \cdot L^{-1}$) (Carignan *et al.*, 2000). Considering that the calcium concentration for saturated calcification in *Daphnia magna* is only reached at 5.2 $mg \cdot L^{-1}$ (Alstad *et al.*, 2000), and that the concentration for survival is in the range of 0.1 to 0.5 $mg \cdot L^{-1}$ (Hessen *et al.*, 2000), the increased calcium concentrations in burnt lakes could have benefited large daphnids.

Second, a decrease in vertebrate predation in burnt lakes relative to reference lakes could explain the increase of large crustaceans observed in burnt lakes. There is some evidence that vertebrate predation on zooplankton could have decreased in burnt lakes since the relative density of small yellow perch (<75 mm) was lower - though not significantly - in impacted lakes (logged and burnt pooled together) relative to reference lakes (St-Onge and Magnan, 2000). However, neither yellow perch nor any other typical planktivorous fish were selected in the environmental RDA model of zooplankton size structure. Additional regression analyses of large crustacean biovlume (dependent variable) against small yellow perch (<75 mm) were not significant ($P = 0.17$).

It is curious that white sucker, a non-planktivorous fish in these lakes, was selected as a good correlate of size spectra variations. The presence of white sucker in Laurentian lakes has previously been associated with decreases in the mean length of *Holopedium gibberum* (a typically large cladoceran) and increases of bosminids (typically small cladocerans) (Rodríguez *et al.*, 1993). Comparison of OPC-derived size spectra with size spectra derived from taxonomic analyses showed that *H. gibberum* was associated with OPC size classes greater than 1100 μm ESD, along with other typically large zooplankton species such as *Daphnia pulex*, *D. catawba*, and *Epischura lacustris* (unpublished data). Hence, the observed negative correlation between white sucker density and biovolume in size classes > 1100 μm is somewhat consistent with results by Rodríguez *et al.* (1993). These authors suggested that white sucker could competitively displace brook trout from its preferred benthos-based food resource to zooplankton. Interestingly, brook trout had a significant influence on size spectra variations, albeit weaker than that of white sucker, TP, and potassium. Brook trout density was positively correlated with biovolume in all size classes, and more so with the larger size classes, which is contrary to what would be expected from size-selective predation on zooplankton (Brooks and Dodson, 1965). The correlational evidence presented here thus offers little evidence that the increase in large crustaceans in burnt lakes could have been the result of decreased vertebrate predation intensity, although it is the most plausible ecological explanation. Indeed, studies on the factors controlling the biomass of zooplankton suggest that crustaceans superior to 1 mm in length, namely *Daphnia*, are under the control of vertebrate predation rather than resource availability (McQueen *et al.*, 1986).

Our results are consistent with those based on size-fractionated limnoplankton organic mass determination (Patoine *et al.*, 2000) whereby the among-group variation in the biomass of zooplankton material collected on a 500 μm mesh-size net (mostly adult crustaceans) was greater than that of the biomass of the 200-500 μm size fraction (copepodites and small cladocerans) Indeed, the biomass of the > 500 μm size fraction was on average 65% higher in burnt-catchment lakes than in reference lakes during the second year following deforestation (P=0.08), while the biomass of the 200-500 μm size fraction was within 20% of reference lakes during both years (P>0.14). Hence, the large crustacean fraction obtained by OPC (> 1100 μm ESD) seems to coincide with the > 500 μm size fraction obtained by sieving, while the small crustacean fraction (< 1100 μm ESD) seems to coincide with the 200-500 μm size fraction. More work, though, is needed to establish a proper correspondence between ESD size classes obtained by OPC and size fractions obtained by sieving of zooplankton material.

It is interesting to note that the same pattern of among-group variations in size spectra and biovolume was observed one and two years after catchment perturbations. Clearly, the effects associated with wildfires are not limited to one year after the passage of wildfires. The prolongation of the effects of catchment deforestation on zooplankton size spectra after the first year following perturbations is consistent with year to year patterns in water quality. These show in fact that the increase in TP, total nitrogen, potassium and chloride observed in perturbed-catchment lakes persisted for at least the first three years following perturbations (Carignan *et al.*, 2000). Further more, increases in logged lakes were generally less than those in burnt lakes, as was also the case here for zooplankton biovolume. In the case of these chemical constituents, the difference in the intensity of effect between logged and burnt lakes could be attributed to the lesser surface areas impacted by logging relative to wildfires (Lamontagne *et al.*, 2000). It is doubtful, however, that the effects of logging and wildfires on zooplankton size structure be simply a function of surface areas impacted. Increased DOC, namely, was greater in logged than in burnt lakes (Carignan *et al.*, 2000), and its influence on size spectra variation, thought weak (Figure 8), should warn us of possible indirect effects of logging on size structure of zooplankton communities. For example, we suggest that, by decreasing light penetration in logged lakes, DOC could act to create a refuge for the larger crustacean organisms against visual vertebrate predators.

Crustacean responses to logging and wildfires seem size-dependent since only the larger crustaceans (> 1100 μm ESD) showed an increase in logged and burnt lakes relative to unperturbed-catchment lakes. Though not always highly significant statistically ($0.02<P<0.07$), these increases represent more than a doubling of biomass of large grazers in logged and burnt lakes relative to reference lakes and most likely represent ecologically significant consequences of logging and wildfires. The mechanisms by which such an increase occurred are a matter of speculation for the moment, but, as discussed above, could involve mortality of zooplanktivorous fish. These results on the effects associated with logging and wildfires on zooplankton represent an advance in our knowledge of the effects of catchment perturbations on aquatic biota. The few studies that have previously considered zooplankton in assessing the ecological effects of logging remained inconclusive with respect to zooplankton, in part because of low catchment surface areas impacted, and in part because of important lake to lake and temporal variability in zooplankton community structure precluding the detection of statistically significant effects (e.g. Rask *et al.*, 1998). Here also, we have observed strong lake to lake and temporal zooplankton variability (Figure 6), and have suggested that impacts of logging on zooplankton may be undetectable at low proportions of catchment logging (Figure 7). The size-based approach to zooplankton community structure, however, did allow us to identify a size fraction where variations were large enough (i.e. more than a doubling of biomass) to be attributed to an effect of logging and wildfires. More work is needed to elucidate the mechanisms by which logging and wildfires induce changes in aquatic communities. Unless variability in zooplankton data is reduced to a minimum by increasing sample size of lakes or increasing sampling frequency, only large effects are likely to be detected. Research is currently under way on a subset of reference lakes whose catchments have recently been logged. Although such a study design eliminates among-lake variability, it introduces among-year variability. The among-year variability observed here was small (< 5 % increase in total biovolume from 1996 to 1997 in reference lakes), and so the prospects for increased statistical power look promising. However, longer-term data suggest that the year factor can be as important as the month factor in zooplankton biomass variability (Yan, 1986). Despite these difficulties related to the variability of zooplankton community structure, size structure analysis was here successful in showing one of the many effects of logging and wildfires on aquatic biota, namely a size shift towards larger crustacean organisms.

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Table 1. Basic limnological characteristics of the three sets of lakes. Mean values are followed by minimum and maximum values. Mean 1996 values are presented for water quality variables.

	Reference lakes (*n*=20 in 1996)	Logged-catchment lakes (*n*=9)	Burnt-catchment lakes (*n*=9)
Percent catchment area logged or burnt	0% 0%-1%	43% 9%-73%	91% 50%-100%
Maximum depth (m)	12.5 7.0-23.0	14.0 5.0-30.0	17.0 10.0-34.0
Mean depth(m)	4.6 2.1-8.9	4.3 2.2-7.5	5.8 4.2-10.0
Lake area (km^2)	0.44 0.15-0.81	0.56 0.18-2.31	0.40 0.17-0.64
Drainage ratio (drainage area/lake area)	5.4 2.3-15.4	6.8 2.0-13.2	7.1 2.5-11.6
pH	5.18 5.15-5.22	5.19 5.15-5.24	5.18 5.14-5.24
Dissolved organic carbon ($mg\bullet L^{-1}$)	5.1 2.8-9.2	8.0 3.0-13.3	5.6 3.1-8.0
Total phosphorus ($\mu g\bullet L^{-1}$)	7.0 4.9-11.8	9.8 5.6-15.8	10.9 5.6-17.3
Potassium ($mg\bullet L^{-1}$)	0.24 (0.08-0.52)	0.55 (0.17-0.95)	0.84 (0.52-1.15)
Chlorophyll-*a* ($\mu g\bullet L^{-1}$)	1.95 0.95-3.24	2.40 1.63-3.26	3.12 1.70-4.24

Table 2. List of environmental variables tested for contribution in among-lake variation in average 1996-1997 crustacean size spectra by RDA. Variables are listed by type (bottom-up or top-down) and by decreasing Percent variance explained. Transformation of environmental variables are indicated by sqrt (square root) or log(x+1).

Variable type	Environmental variable	Units	Abbreviation	Mean	Min	Max	Occurrence on 38 lakes	Percent variance explained	*P*
Bottom-up	Potassium, sqrt	µg•L^{-1}	K	3.22	0.86	9.54		13.9	0.00
	Ammonium, sqrt	µg•L^{-1}	NH4	258.00	65.93	4205.84		10.0	0.01
	Nitrate, log (x+1)	µg•L^{-1}	NO3	4.53	0.38	245.56		9.4	0.01
	Total phosphorus, log (x+1)	µg•L^{-1}	TP	7.86	4.83	15.72		8.7	0.01
	Chloride, sqrt	µg•L^{-1}	Cl	1.76	1.04	3.50		8.1	0.02
	Total nitrogen, log (x+1)*	µg•L^{-1}	TN	246.61	146.56	619.11		7.2	0.04
	Magnesium, sqrt	µg•L^{-1}	Mg	3.86	2.20	7.61		6.8	0.04
	Chlorophyll-a	µg•L^{-1}	chl-a	2.09	1.17	4.32		4.7	0.12
	Nitrogen to phosphorus ratio, log (x+1)		NP	31.79	20.55	42.33		4.7	0.15
	Chlorophyll-a / TP ratio		chl-a/TP	0.278	0.153	0.402		4.6	0.13
	Sulfate, log (x+1)	µg•L^{-1}	SO4	0.98	0.51	1.86		3.3	0.27
	Sodium, log (x+1)	µg•L^{-1}	Na	0.64	0.38	1.01		2.8	0.35
	Calcium, log (x+1)	µg•L^{-1}	Ca	1.60	1.00	2.75		2.7	0.39
	pH		pH	6.43	5.67	7.00		1.5	0.69
	Dissolved organic carbon, log (x+1)	mg•L^{-1}	DOC	5.57	2.68	12.73		1.3	0.78

Variable type	Environmental variable	Units	Abbreviation	Mean	Min	Max	Occurrence on 38 lakes	Percent variance explained	*P*
Top-down	White sucker (*Catostomus commersoni*)	CPUE	Caco	4.9	0.0	36.3	31	9.8	0.01
	Brook trout (*Salvelinus fontinalis*)	CPUE	Safo	1.9	0.0	38.8	7	7.0	0.04
	Pearl dace (*Semotilus margarita*)	CPUE	Sema	7.1	0.0	145.7	7	5.4	0.10
	Walleye (*Stizostedion vitreum*)	CPUE	Stvi	1.7	0.0	15.1	9	4.2	0.15
	Chaoborus larvae, log (x+1)	ind•m^{-3}	Chaob	32.4	0.0	174.1	36	3.8	0.22
	Lake whitefish (*Coregonus clupeaformis*)	CPUE	Cocl	1.7	0.0	18.2	11	3.0	0.34
	Lake chub (*Couesius plumbeus*)	CPUE	Copl	2.6	0.0	35.0	5	2.5	0.41
	Various unidentified cyprindids	CPUE	Cysp	1.4	0.0	40.2	10	2.0	0.49
	Fallfish (*Semotilus corporalis*)	CPUE	Seco	0.8	0.0	14.5	10	1.5	0.71
	Northern pike (*Esox lucius*)	CPUE	Eslu	1.5	0.0	5.5	27	1.4	0.76
	Yellow perch (*Perca flavescens*)	CPUE	Pefl	9.9	0.0	133.2	25	1.3	0.77
	Golden shiner (*Notemigonus crysoleucas*)	CPUE	Nocr	3.6	0.0	84.5	5	1.2	0.81
	Finescale dace (*Chrosomus neogaeus*)**	CPUE	Phne	1.7	0.0	54.3	5	1.1	0.77
	Burbot (*Lota lota*)	CPUE	Lolo	0.1	0.0	0.8	7	1.0	0.87

* Total nitrogen measurements were missing for the June and July 1997 sampling periods.

**Previously *Phoxinus neogaeus* (Cope).

Table 3. RDA of average size spectra in relation to catchment condition. A separate analysis was conducted for the 1996 average size spectra and the 1997 average size spectra. Within each year, pairwise comparisons were performed between reference lakes and burnt-catchment lakes (R vs. B), reference lakes and logged-catchment lakes (R vs. C), and logged- and burnt-catchment lakes (C vs. B).

Species matrix Y	Number of eigenvalues	% variance explained	Probability value (999 permutations)
Size spectra 96	2	13.4	0.029
Size spectra 96: R vs. B	1	13.8	0.021
Size spectra 96: R vs. C	1	8.2	0.081
Size spectra 96: C vs. B	1	3.7	0.575
Size spectra 97*	2	14.5	0.019
Size spectra 97: R* vs. B	1	17.5	0.008
Size spectra 97: R* vs. C	1	5.5	0.249
Size spectra 97: C vs. B	1	7.9	0.213

* Analyses of 1997 size spectra had four reference lakes omitted because these had their catchments logged following the first 1996 sampling year, and could thus no longer be considered as reference lakes.

Table 4. Analyses of variance of crustacean biovolume < 1100 μm, crustacean biovolume > 1100 μm, total biovolume and mean size as a function of catchment condition for A) 1996 (one year after catchment perturbations) and B) 1997 (two years after perturbations). Mean values for the reference, logged and burnt groups were back-calculated from log(x+1)-transformed data. Groups with different letters are significantly different at the 5% level. Variance components of the lake (error term) and month (residual) factors are given in percentages.

A) One year after catchment perturbations

	Reference	Logged	Burnt	$F_{2,35}$	*P*	Var lake	Var month
“Small” biovolume	524	480	610	0.89	0.41	5%	95%
	a	a	a				
“Large” biovolume	32	109	149	4.25	0.022	27%	73%
	a	ab	b				
Total Biovolume	652	692	886	1.55	0.23	6%	94%
	a	a	a				
Mean size	652	777	789	3.10	0.058	37%	63%
	a	a	a				

B) Two years after catchment perturbations

	Reference	Logged	Burnt	$F_{2,31}$	*P*	Var lake	Var month
“Small” biovolume	565	557	672	0.50	0.61	15%	85%
	a	a	a				
“Large” biovolume	25	68	122	3.86	0.032	17%	83%
	a	ab	b				
Total Biovolume	660	709	955	2.05	0.15	1%	99%
	a	a	a				
Mean size	622	681	784	3.52	0.042	29%	71%
	a	ab	b				

Figure 1. PCA plots based on the analysis of the 228 zooplankton size spectra. A) Plot of the 22 size classes vectors. Numbers represent size classes (e.g. 2 represents the 200-300 µm size class and so on). The length of the projection of a size-class vector on principal component axis I or II indicates how much it contributes to the sample ordination in two dimensions relative to other vectors. The equilibrium circle (radius=0.30) indicates the length of a size-class vector contributing equally to all 22 principal component axes. Size-class vectors longer than the equilibrium circle contribute significantly to the ordination of samples in the plane of the first two principal component axes. B) Ordination plot of the 228 samples coded according to catchment condition. Samples identified by name have their size spectra illustrated on the following figure.

Figure 1A)

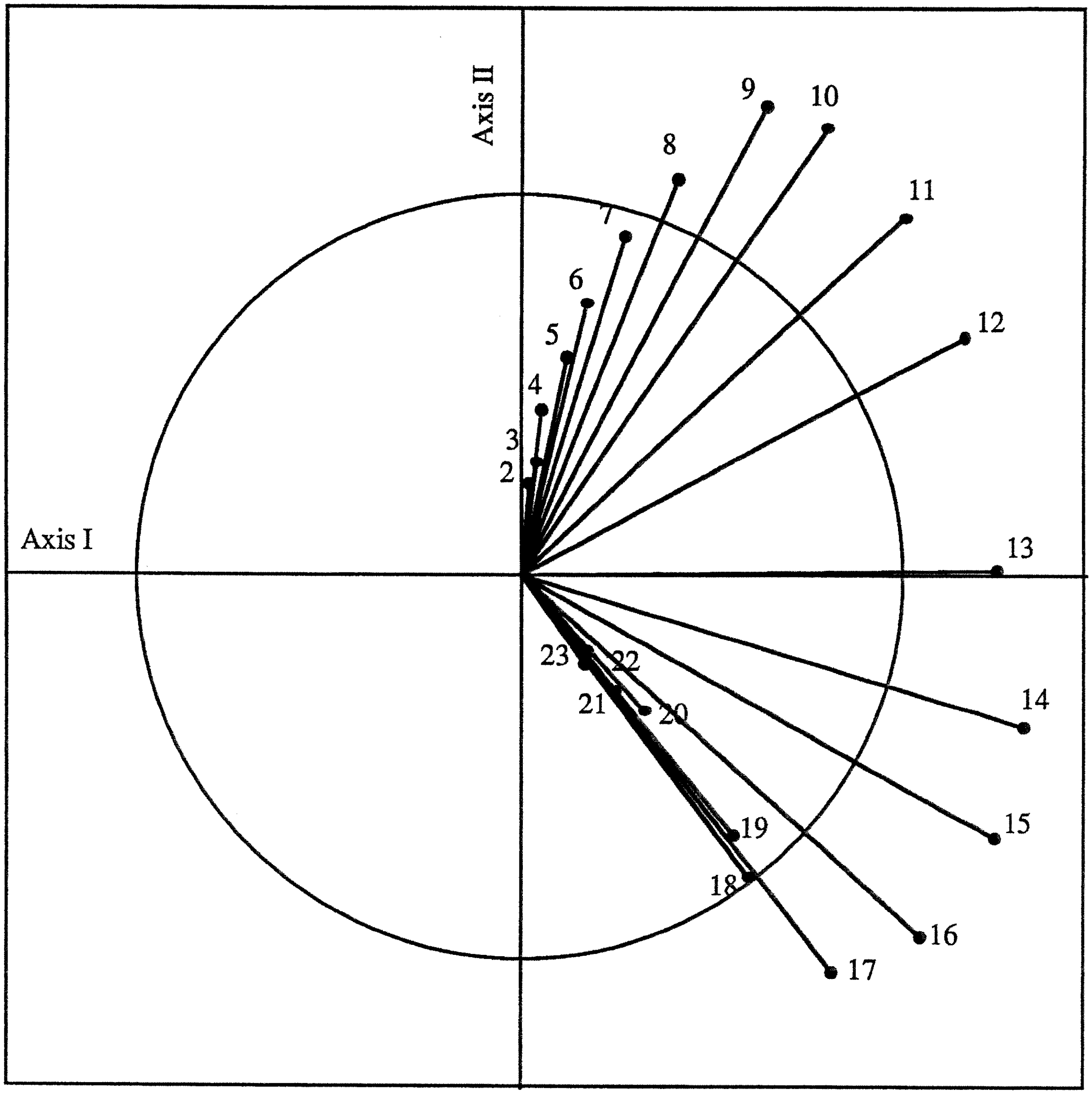


Figure 1B)

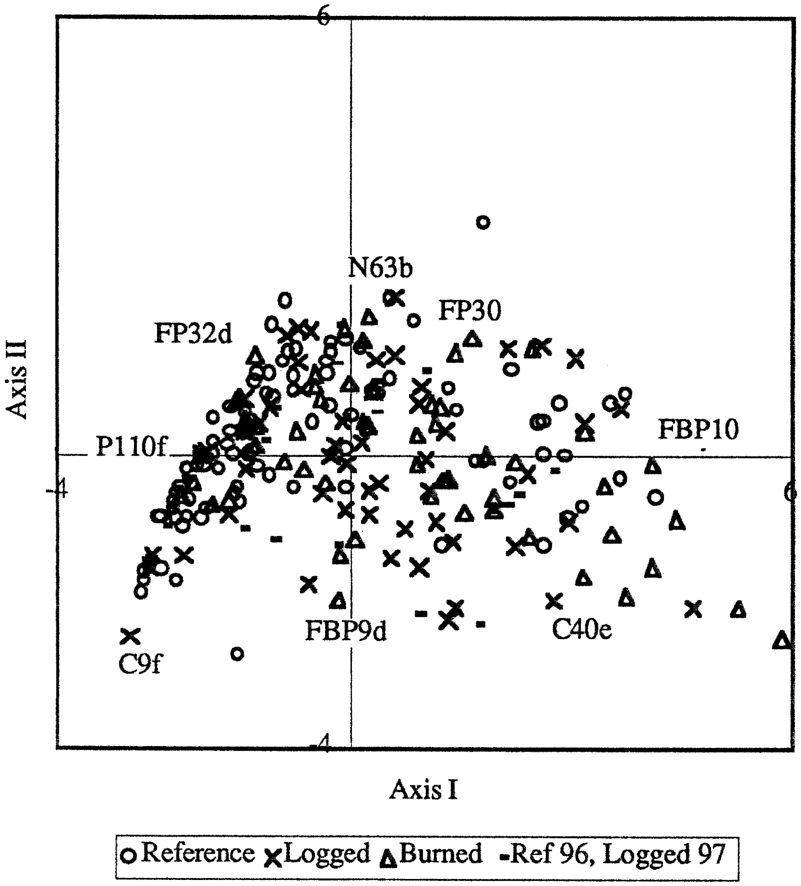
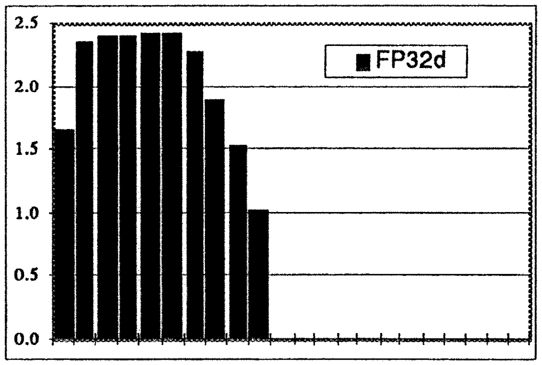
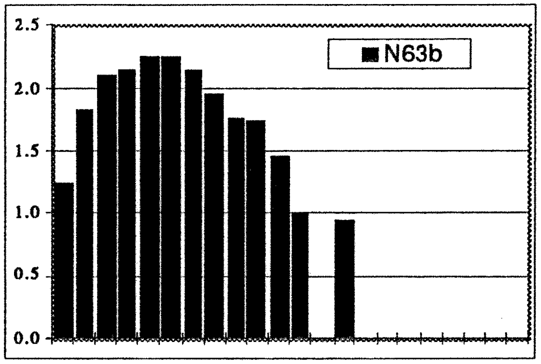
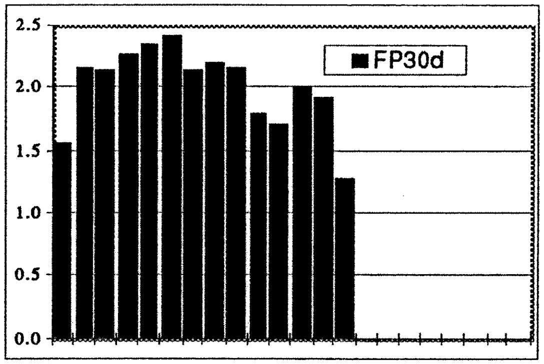
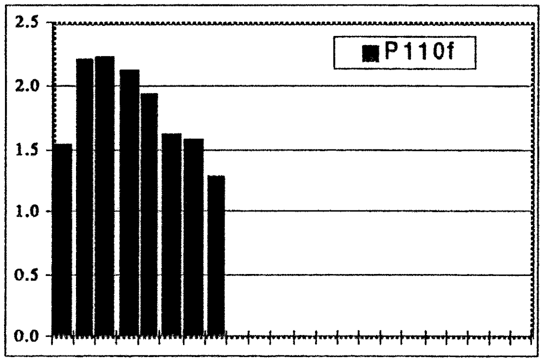

6
N63b
FP30
FP32d
P110f
FBP10
-4
6
FBP9d
C40e
C9f
-4
Axis II
Axis I
○ Reference ✕ Logged △ Burned - Ref 96, Logged 97

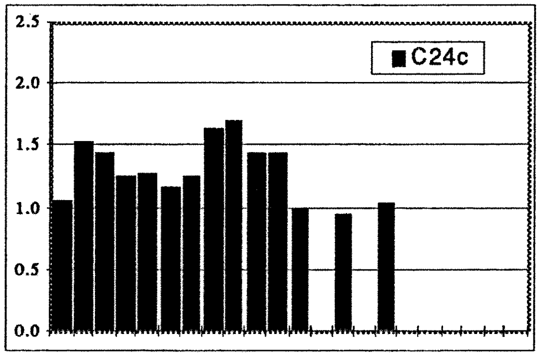
Figure 2. Examples of size spectra that illustrate how biovolume in each size class changes as one progress from low axis I PCA scores (left-most column) to high ones (right-most column), and from low axis II PCA scores (bottom row) to high ones (upper row). The abscissa represents 22 size classes, from 200-300 µm to 2300-2400 µm in equivalent spherical diameter. The vertical axis represents crustacean biovolume on a log(x+1) transformed scale of $mm^3 \bullet m^{-3}$ units.

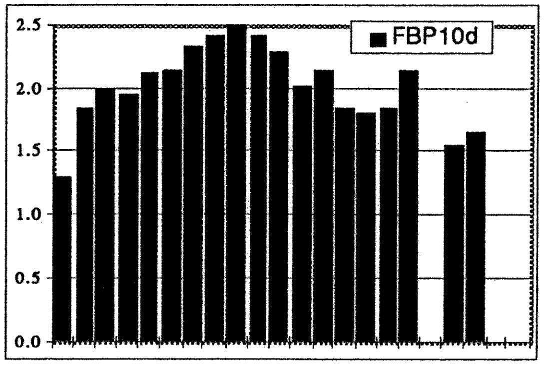

2.5
2.0
1.5
1.0
0.5
0.0
■ FP32d

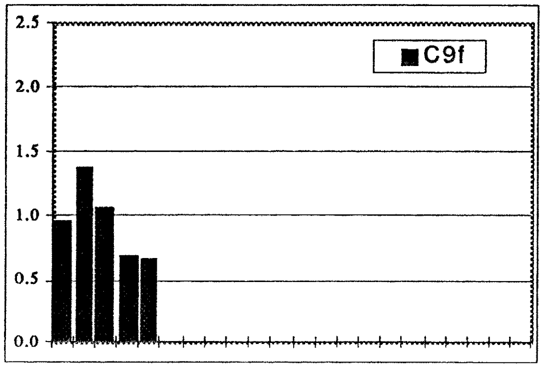

2.5
2.0
1.5
1.0
0.5
0.0
■ N63b

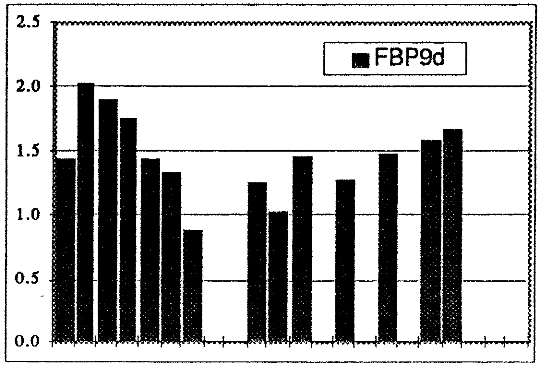

2.5
2.0
1.5
1.0
0.5
0.0
■ FP30d


2.5
2.0
1.5
1.0
0.5
0.0
■ P110f


2.5
2.0
1.5
1.0
0.5
0.0
■ C24c


2.5
2.0
1.5
1.0
0.5
0.0
■ FBP10d


2.5
2.0
1.5
1.0
0.5
0.0
■ C9f


2.5
2.0
1.5
1.0
0.5
0.0
■ FBP9d

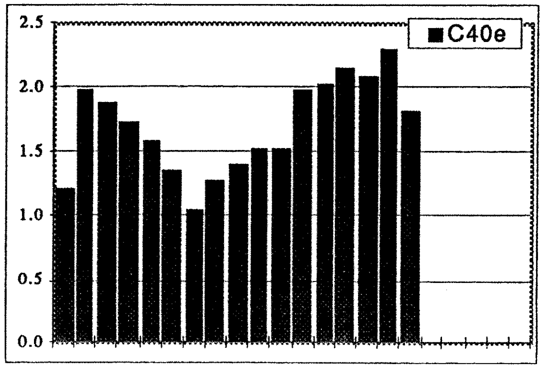

2.5
2.0
1.5
1.0
0.5
0.0
■ C40e

Figure 3. RDA ordination of zooplankton size spectra for the year 1996 in relation to dummy variables coding for catchment condition. A) Ordination in size class space. Size class vectors are represented by dots instead of arrows and their coordinates are divided in half for clarity. Numbers represent size classes (e.g. 2 represents the 200-300 µm size class and so on). Capital letters code for the centroids of reference lakes (R), logged-catchment lakes (C), and burnt-catchment lakes (B).

Figure 3A)

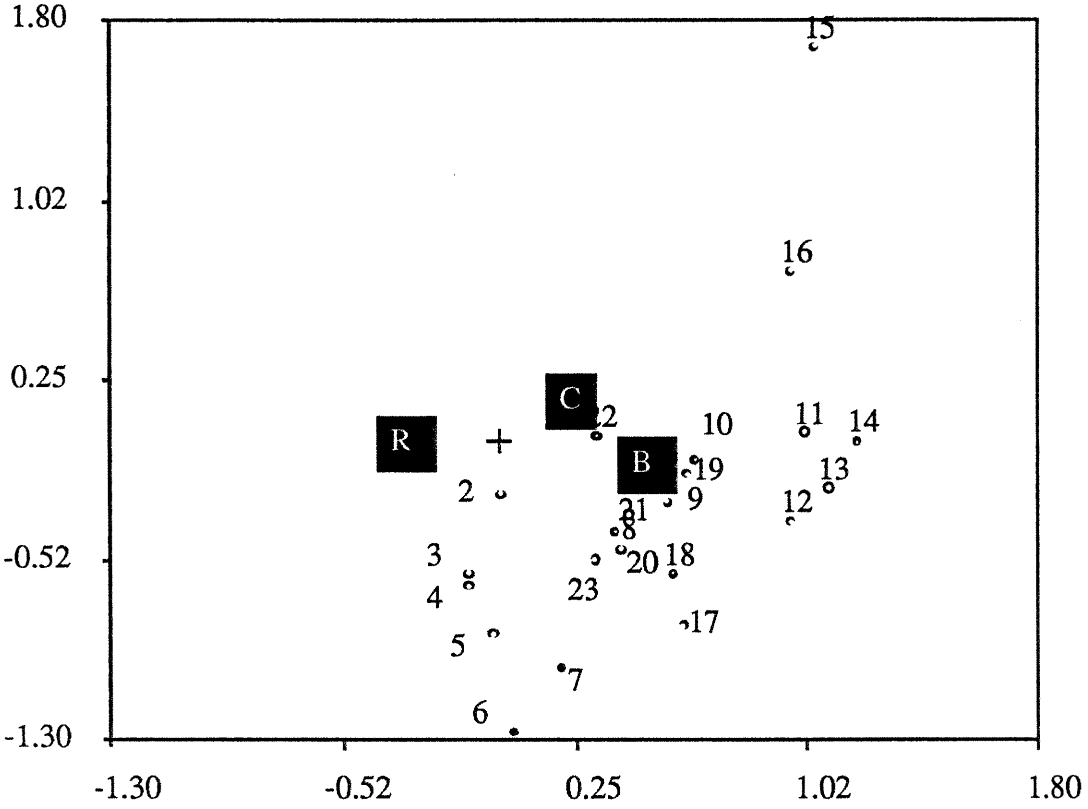

1.80
1.02
0.25
-0.52
-1.30
-1.30
-0.52
0.25
1.02
1.80
R
C
B
+
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Figure 3B)

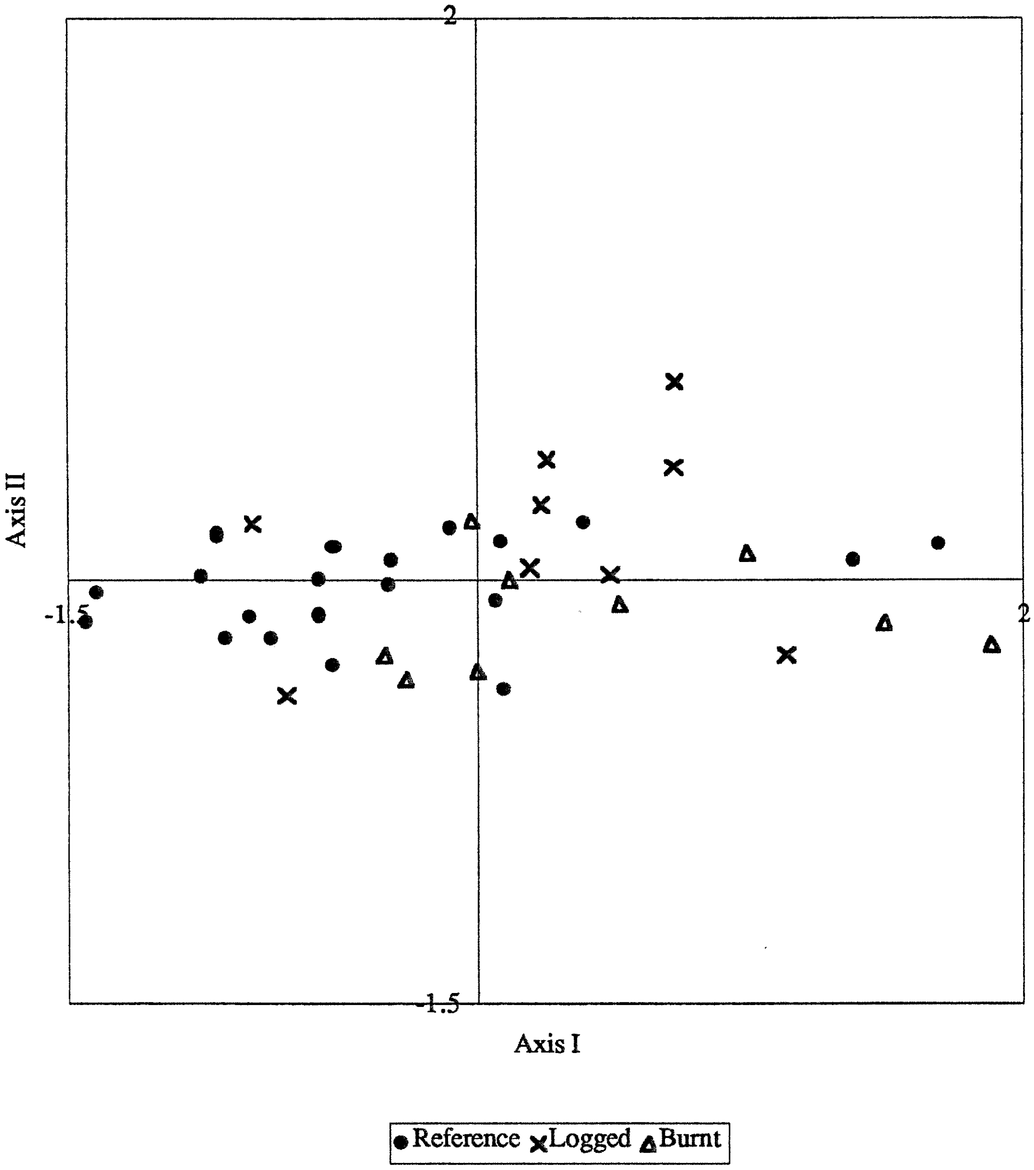


Figure 4. Average size spectra by catchment type for the year 1996. Biovolume is expressed as log(x+1) of $mm^3 \cdot m^{-3}$ for each size class from 200-300 µm to 2300-2400 µm ESD. Size classes most strongly associated with burnt-catchment lakes based on RDA analysis (Figure 3) have stippled bars. Error bars represent 95% confidence intervals on the mean.

Figure 4.

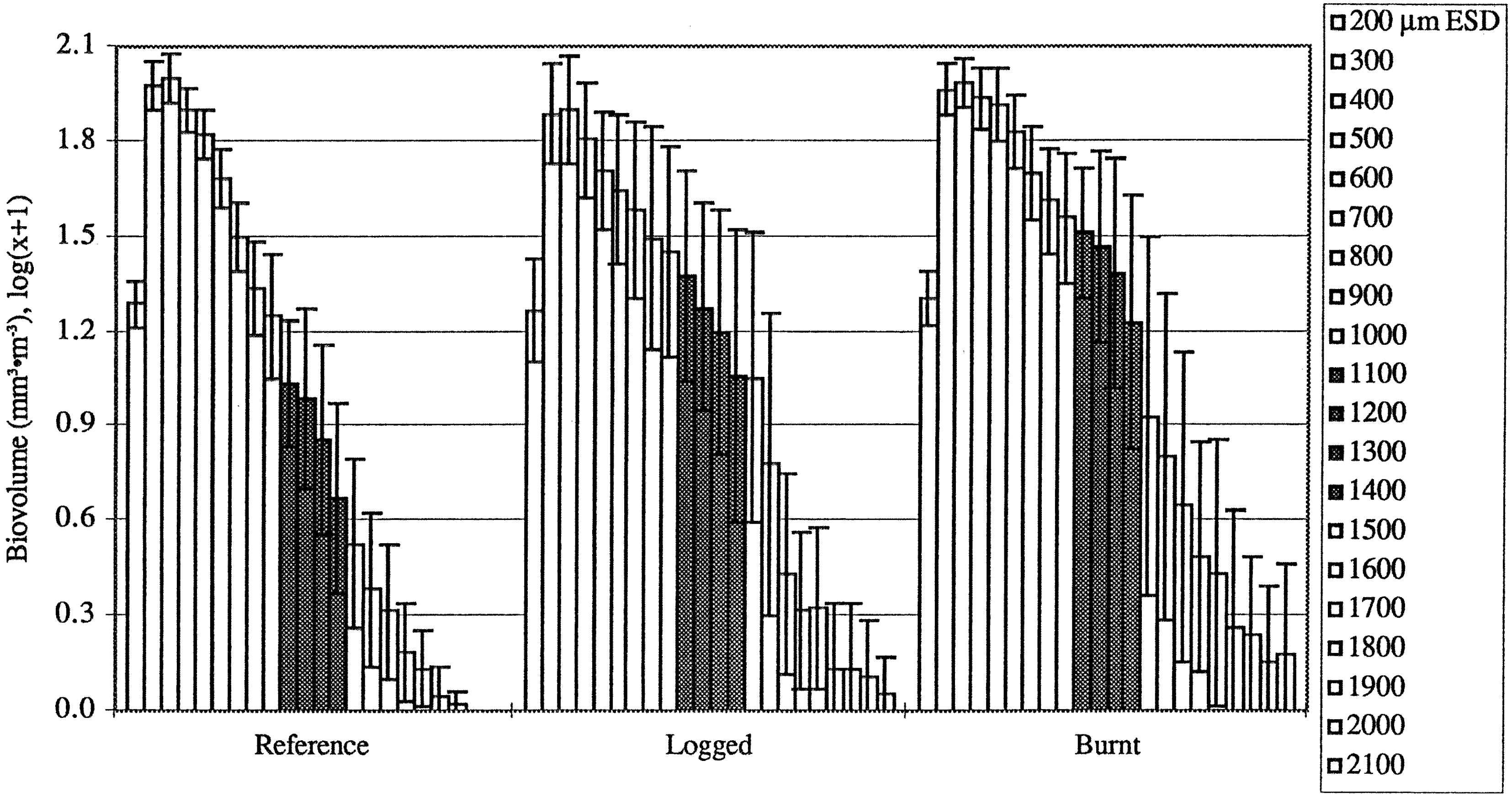

2.1
1.8
1.5
1.2
0.9
0.6
0.3
0.0
Biovolume (mm³•m⁻³), log(x+1)
Reference
Logged
Burnt
200 µm ESD
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
1700
1800
1900
2000
2100

Figure 5. Box plots illustrating among-group differences in A) biovolume < 1100 μm ESD; B) biovolume > 1100 μm ESD; C) total biovolume; D) crustacean community mean size, in 1996 and 1997. Boxes with different letters are significantly different at the 5% level. Boxes represent 25th and 75th quantiles. The line across the middle of the box identifies the median. Whiskers extend from the 10th to the 90th quantiles. Open boxes represent reference lakes; hatched boxes represent logged lakes; shaded boxes represent burnt lakes.

Figure 5

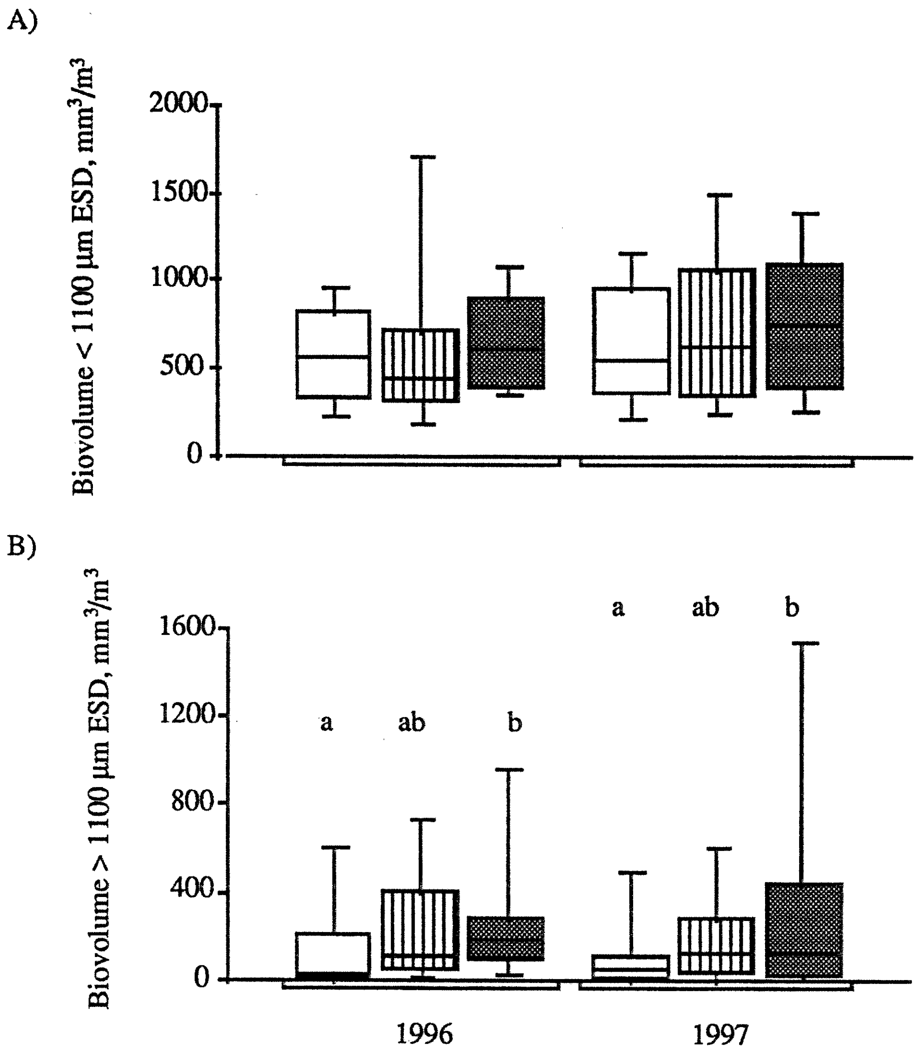

A)
Biovolume < 1100 µm ESD, mm³/m³
2000
1500
1000
500
0
B)
Biovolume > 1100 µm ESD, mm³/m³
1600
1200
800
400
0
a
ab
b
a
ab
b
1996
1997

Figure 5

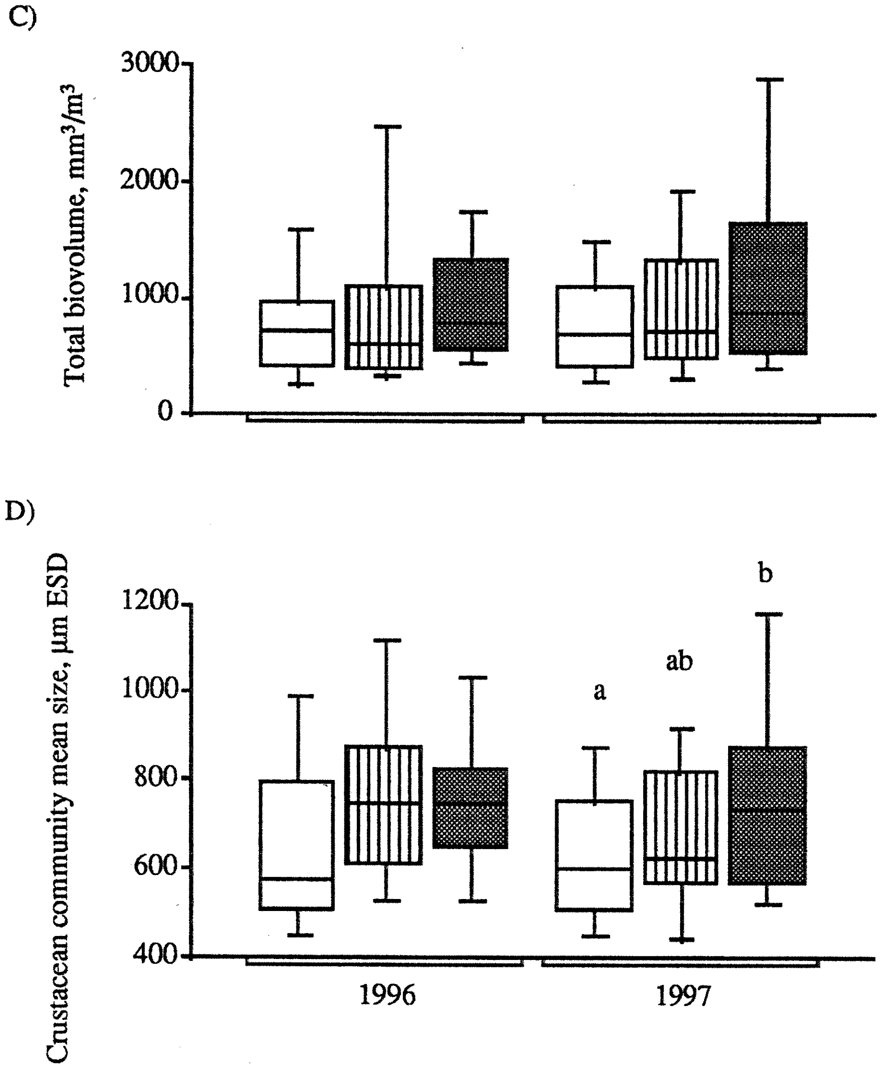

C)
Total biovolume, mm^3/m^3
3000
2000
1000
0
D)
Crustacean community mean size, µm ESD
1200
1000
800
600
400
a
ab
b
1996
1997

Figure 6. Box plots illustrating among-group and among-month variations in A) biovolume < 1100 μm ESD; B) biovolume > 1100 μm ESD; C) total biovolume; D) crustacean community mean size. Boxes with different letters are significantly different at the 5% level. Boxes represent 25th and 75th quantiles. The line across the middle of the box identifies the median. Whiskers extend from the 10th to the 90th quantiles. Whiskers extend from the 10th to the 90th quantiles. Open boxes represent reference lakes; hatched boxes represent logged lakes; shaded boxes represent burnt lakes.

Figure 6

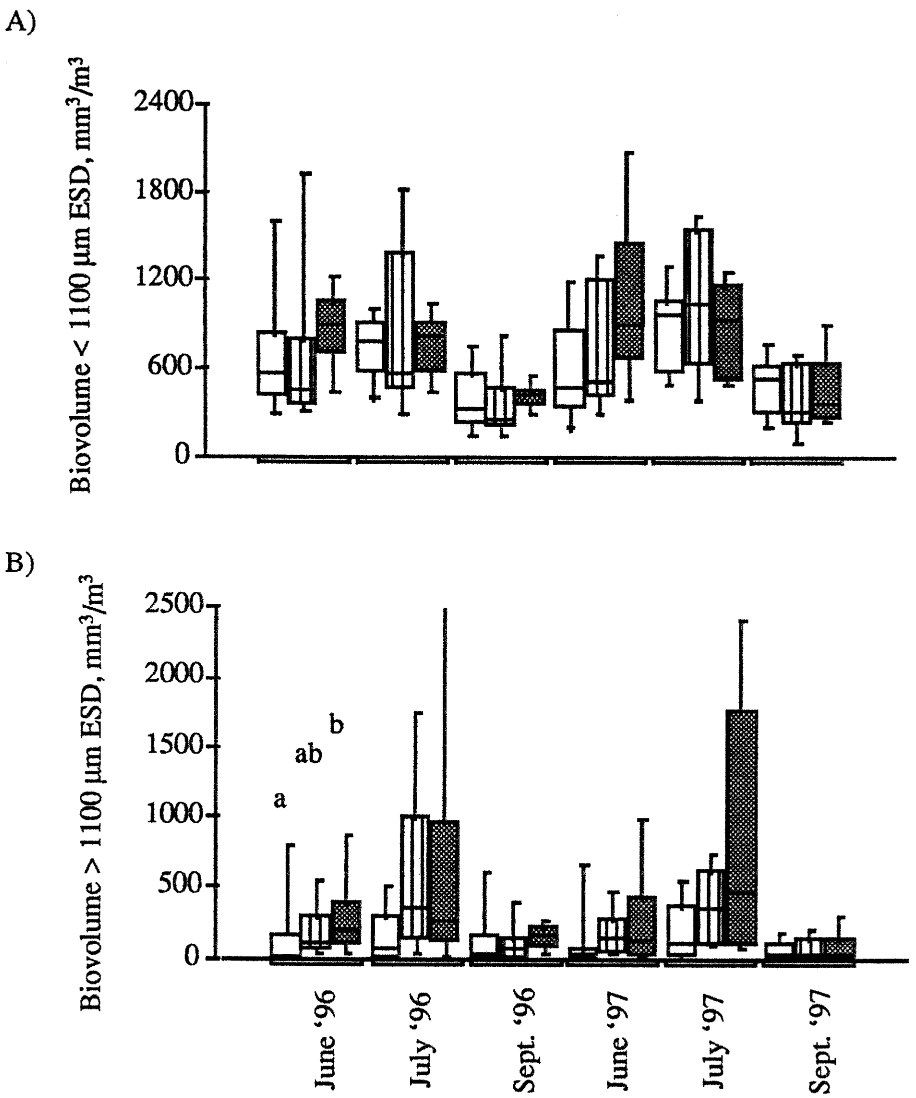

A)
Biovolume < 1100 µm ESD, mm³/m³
2400
1800
1200
600
0
B)
Biovolume > 1100 µm ESD, mm³/m³
2500
2000
1500
1000
500
0
a
ab
b
June '96
July '96
Sept. '96
June '97
July '97
Sept. '97

Figure 6

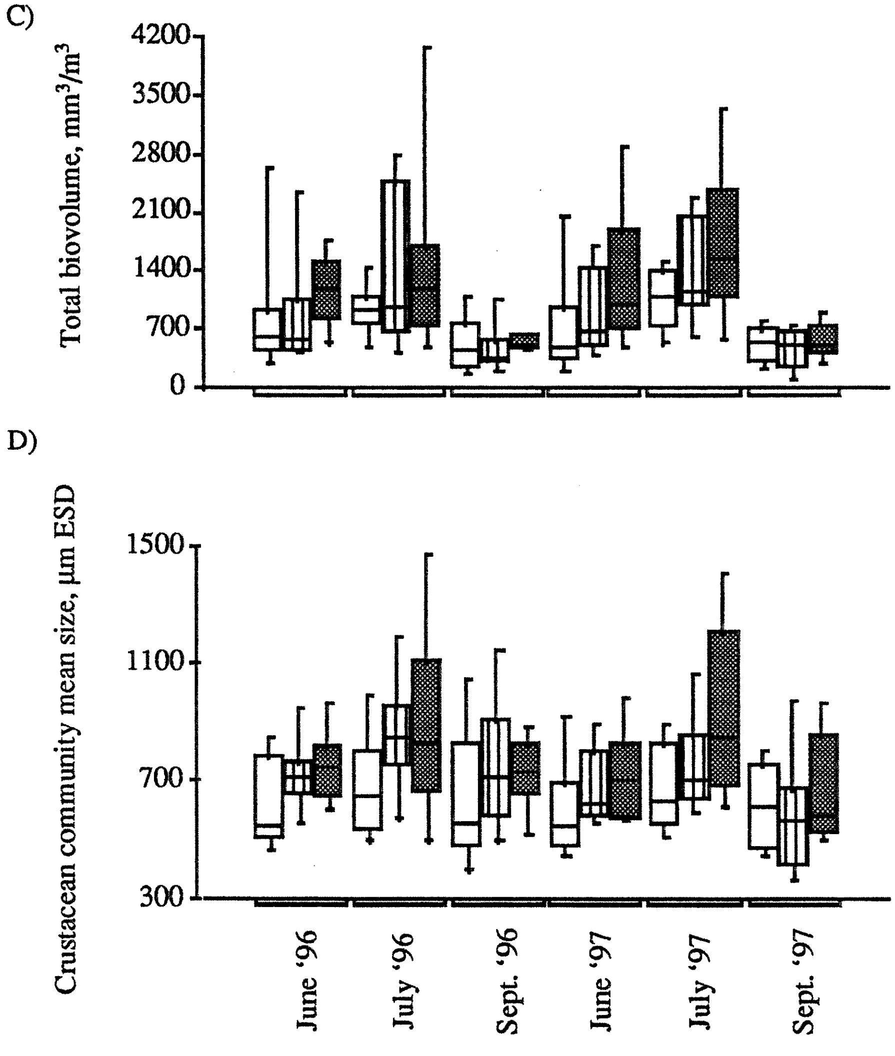

C)
Total biovolume, mm3/m3
4200
3500
2800
2100
1400
700
0
D)
Crustacean community mean size, µm ESD
1500
1100
700
300
June '96
July '96
Sept. '96
June '97
July '97
Sept. '97

Figure 7. Regression plot of the biovolume of small crustacean (< 1100 µm ESD, log(x+1) of $mm^3 \cdot m^{-3}$) against percent catchment area logged or burnt (arcsin(sqrt(x)), one year after disturbances. Logged lakes are represented by crosses; burnt lakes by triangles. Regression equation for the logged group (*n*=9): Y = 0.012±0.005 (X) + 2.23±0.23; r^2=40%; root mean square error: 0.22; *P*=0.066. Regression equation for the logged and burnt groups (*n*=18): Y = 0.004±0.002 (X) + 2.51±0.12; r^2=23%, root mean square error: 0.12; *P*=0.042. The regression coefficient for the burnt group of lakes was not significant (*P*=0.46).

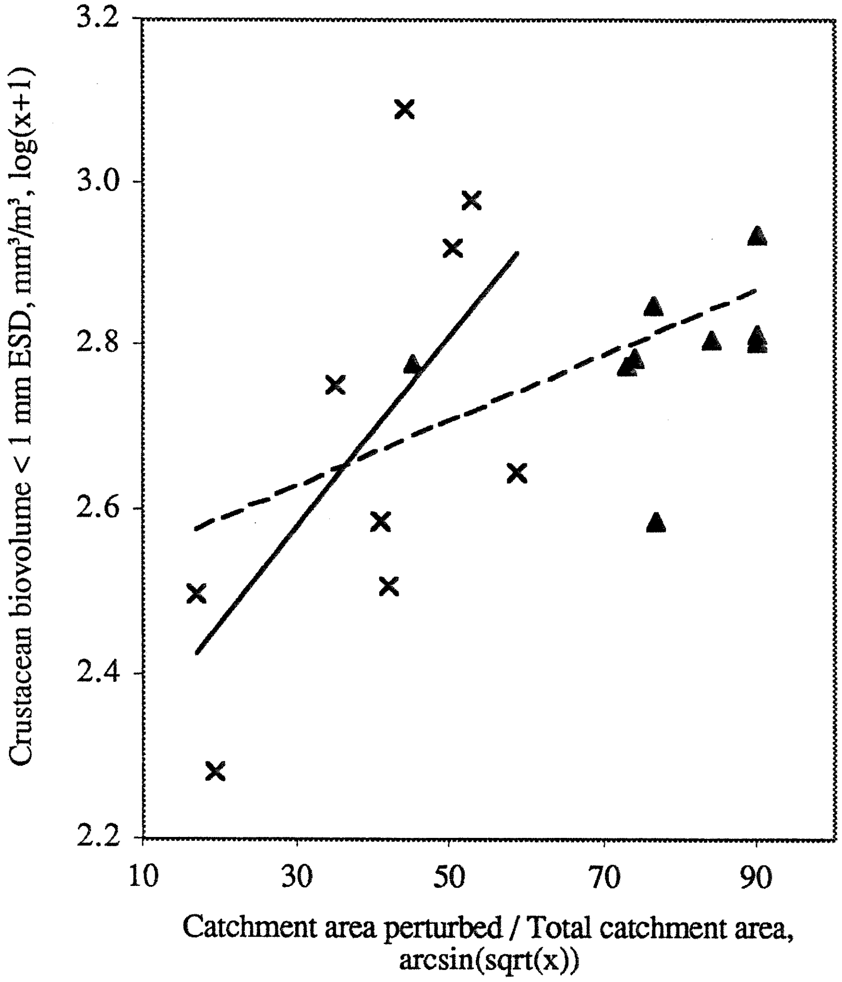
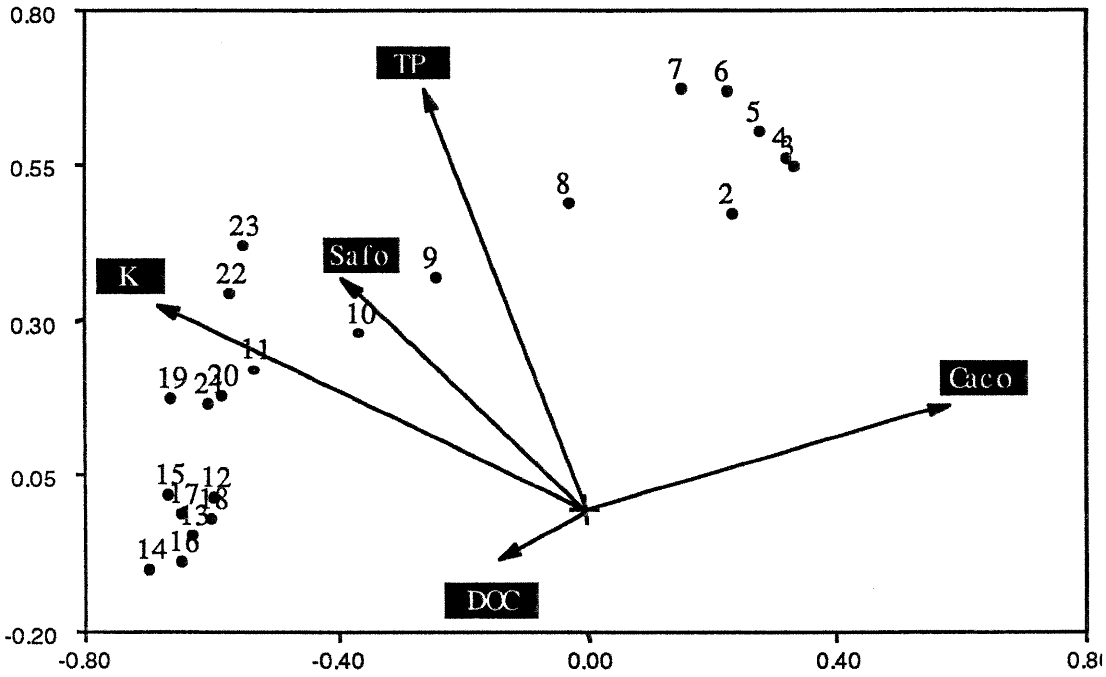
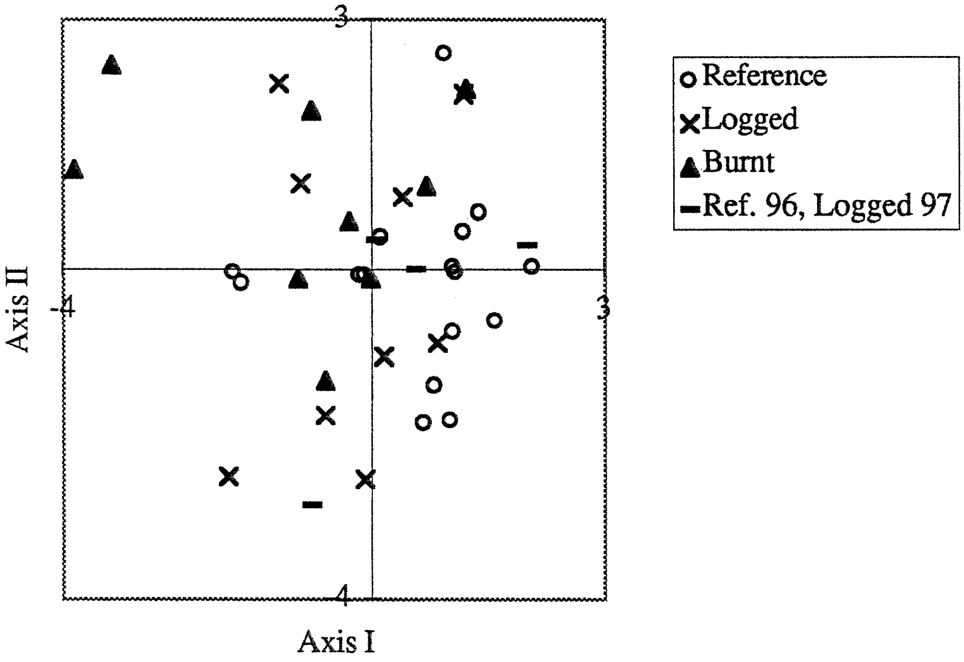


Figure 8. RDA ordination plots of 38 average size spectra as a function of bottom-up and top-down variables. A) Ordination in size class space: numbers represent the tip of size classes vectors (e.g. 2 represents the 200-300 µm size class vector and so on). Labels of environmental vectors are depicted in inverse, and are abbreviated according to Table 2. An angle near 0° between a size class and an environmental vector indicates strong positive correlation of size class biovolume with the environmental factor whereas an angle near 180° indicates strong negative correlation. B) Ordination in lake space; circles represent reference lakes (*n*=16); crosses represent logged-catchment lakes (*n*=9); triangles represent burnt-catchment lakes (*n*=9); dashes represent lakes whose catchment were logged between the ice-free season of 1996 and that of 1997 (*n*=4).

Figure 8A)


0.80
0.55
0.30
0.05
-0.20
-0.80
-0.40
0.00
0.40
0.8
TP
Safo
K
Caco
DOC
7
6
5
4
3
2
8
9
10
11
19
21
20
22
23
15
12
17
18
13
14
16

B)


3
-4
3
4
Axis II
Axis I
○ Reference
× Logged
▲ Burnt
– Ref. 96, Logged 97

Conclusion générale

La coupe forestière entraîne-t-elle des changements dans la structure des communautés zooplanctoniques et, si oui, comment ces changements se comparent-ils à ceux occasionnés par les feux de forêt? Voilà la question qui a motivé cette recherche, et à laquelle cette thèse apporte quelques éléments de réponse.

Les connaissances sur les effets des coupes et des feux portent dans une large mesure sur le flux des éléments nutritifs du sol vers les plans d'eau, puisque c'est là que se situe vraisemblablement une des conséquences immédiates des coupes et des feux. Par ailleurs, les connaissances sur l'écologie du zooplancton portent, entre autres, sur l'influence des éléments nutritifs et de diverses perturbations environnementales autres que les coupes ou les feux sur la biomasse, la richesse et la structure en taille du zooplancton. Les hypothèses que nous avons formulées concernant les effets attendus des coupes et des feux sur les communautés zooplanctoniques se basaient sur ce corpus disparate de connaissances. Dans l'ensemble, les trois hypothèses que nous avons formulées ont été infirmées, ce qui témoigne du manque de connaissances sur le comportement du zooplancton en réaction aux perturbations environnementales. Néanmoins, il en résulte que nous en savons plus aujourd'hui sur les effets des coupes et des feux. Revoyons ces hypothèses une à une.

Premièrement, nous nous attendions à ce que la biomasse du zooplancton dans les lacs perturbés soit plus élevée que dans les lacs de référence. Une telle hypothèse se fondait, d'une part, sur le fait que les coupes et les feux entraînent généralement une augmentation des éléments nutritifs dans les cours d'eau et que, d'autre part, concentration en éléments nutritifs et biomasse du zooplancton vont de pair. Bien que la première proposition ait été vérifiée (Carignan, D'Arcy & Lamontagne, 2000), la biomasse totale du zooplancton dans les lacs coupés ou brûlés ne différait pas de celle des lacs de référence (Chapitre I), probablement parce que la seconde proposition ne tenait pas. En effet, la relation entre la biomasse du limnoplancton > 500 µm (surtout des crustacés) et la concentration de phosphore totale dans les lacs de référence était généralement faible (r^2=19%) (Figure 1A). La décomposition ultérieure de la biomasse totale du zooplancton en ses différents groupes taxonomiques ou en différentes fractions de taille a toutefois permis de déceler certaines composantes du zooplancton particulièrement sensibles aux perturbations des bassins versants. Les calanoïdes, dont la biomasse a décru dans les lacs coupés (–43%), et le micro-plancton, dont la biomasse a presque doublé (+90%) dans les lacs brûlés illustrent ce point. Non moins important, nous avons démontré dans le premier chapitre que seules des différences de biomasse de l'ordre de 40% à 100% et plus pouvaient être déclarées statistiquement significatives et donc attribuables à un effet des perturbations. De telles analyses de puissances sont rarement rapportées dans les travaux d'écologie. Pourtant, elles permettent de nuancer la conclusion selon laquelle le phénomène étudié (ici les coupes) n'a pas d'effet sur le sujet (ici la biomasse totale du zooplancton) en y associant un degré de certitude. Le degré de certitude quant à l'absence d'effet des perturbations sur la biomasse totale du zooplancton était faible (Chapitre I), en partie à cause de la forte variabilité des données. Le moment de l'échantillonnage (juin, juillet ou septembre) était une source importante de variabilité des données qui diminuait la force des relations entre la biomasse du zooplancton et les facteurs environnementaux. Par exemple, la faiblesse des relations entre la biomasse du zooplancton et la concentration de phosphore (r^2<20%, 0.05<P<0.10) était en partie due à une forte variabilité saisonnière (Figure 1). Une telle variabilité intra-lac s'est ajoutée à la variabilité inter-lacs, de telle sorte que seules des différences supérieures à 40% par rapport aux lacs de référence ont pu être déclarées significatives (à α=0,05), comme ce fut le cas pour les calanoïdes et le micro-plancton.

Nous avons postulé, dans le deuxième chapitre, que les variations inter-groupes dans la biomasse de certains groupes taxonomiques (les calanoïdes et les rotifères) pouvaient masquer des variations plus importantes encore au niveau des assemblages d'espèces. Nous postulions également, sur la base des travaux de Odum (1969, 1985), que la richesse en espèces des lacs perturbés serait moindre que dans les lacs de référence. Or, ni l'une ni l'autre de ces prédictions n'a été confirmée par les résultats. Ici encore, le facteur temps (mois d'échantillonnage) était une source importante de variation au sein d'un même lac, du moins en ce qui concerne les assemblages d'espèces. Encore une fois, il semblerait que la variabilité temporelle dans un lac s'est traduite par une grande variabilité entre les lacs d'un même groupe et rendait les variations en assemblages d'espèces observées entre les groupes de lacs non significatives. Ainsi, les variations au niveau de la biomasse de grands groupes taxonomiques cachent bel et bien des variations encore plus fortes au niveau des assemblages d'espèces; seulement, cette variation est de nature temporelle, et non pas de nature environnementale comme nous l'avions envisagé initialement. Par conséquent, les résultats des analyses taxonomiques ont été les moins aptes à mettre en relief les différentes conditions de bassins versants, bien qu'ayant exigé un effort d'analyse en laboratoire plus grand que la mesure des poids secs ou la détermination des spectres de taille. L'analyse taxonomique s'est néanmoins révélée nécessaire pour caractériser les résultats obtenus par les deux autres méthodes.

Toujours sur la base des travaux de Odum (1969, 1985), nous avons postulé, dans le troisième chapitre, que la structure en taille des communautés de crustacés zooplanctoniques serait déplacée vers des organismes de plus petite taille dans les lacs perturbés. C'est effectivement sous l'angle de la structure en taille que la condition du bassin versant s'est révélée être une source de variation importante. Étonnamment, les résultats étaient en contradiction avec nos prédictions: nous avons observé dans les lacs brûlés et, dans une moindre mesure, dans les lacs coupés, un déplacement vers les organismes de grande taille. La valeur heuristique des prédictions de Odum n'est pas remise en question, pas plus que les travaux antérieurs ayant démontré une diminution de la taille moyenne des communautés zooplanctoniques soumises à diverses perturbations environnementales (Sprules & Munawar, 1986; Harig & Bain, 1998; Schindler, 1990; Havens & Hanazato, 1993). Justement, ces travaux ont tous comme point commun l'étude de perturbations qui altèrent l'environnement physique ou chimique du zooplancton, tout en laissant l'environnement biotique – notamment les poissons – inaltéré (ou non examiné). Or, dans le cas présent, le déplacement vers des crustacés de grande taille dans les lacs perturbés pourrait être la conséquence de la mortalité rapportée chez les jeunes poissons planctivores de certaines espèces (St-Onge & Magnan, 2000), bien qu'il ne nous ait pas été possible d'appuyer une telle hypothèse par des relations entre la densité de poissons et la biomasse des grands crustacés (Chapitre III). Ainsi, c'est plutôt un déplacement vers les grandes tailles qui semble caractériser les perturbations de bassins versants sur les communautés zooplanctoniques et les communautés de poissons. L'idée qui veut qu'une perturbation soit associée à un déplacement vers les organismes de petite taille semblerait donc faire abstraction des interactions trophiques qui déterminent en partie la structure en taille des communautés.

D'une manière générale, il semble que les feux soient associés à une augmentation de la biomasse de certaines fractions de taille du zooplancton par rapport aux lacs de référence, notamment le micro-plancton (algues, rotifères, nauplii) (Chapitre I) et les crustacés de grande taille (Chapitre III). Ces augmentations de biomasse dans les extrémités de taille de la communauté zooplanctonique s'interprètent bien comme étant une conséquence des changements rapportés dans les maillons trophiques inférieurs et supérieurs: augmentation du micro-plancton associée aux apports en éléments nutritifs en provenance du bassin versant (Figure 1B); augmentation des crustacés de grande taille qui coïncide avec une mortalité des petits poissons planctivores (Chapitre III). Ces interprétations demeurent toutefois spéculatives puisqu'aucune relation forte n'a pu être établie entre la biomasse du micro-plancton et les éléments nutritifs d'une part, et entre la biomasse des grands crustacés et la densité de poissons planctivores d'autre part. Rappelons que le but de cette étude n'était pas de mettre à jour des mécanismes, mais plutôt de vérifier si les coupes et les feux entraînent un changement dans la structure des communautés zooplanctoniques. Par ailleurs, la diminution de petits individus de poissons planctivores dans les lacs perturbés et l'augmentation concomitante de grands crustacés va dans le même sens qu'une des prédictions de Schindler (1987), à savoir qu'une altération dans la structure des communautés de poissons a de fortes chances de se répercuter rapidement sur les maillons trophiques inférieurs.

La grande variabilité temporelle du zooplancton dans les lacs étudiés, tant dans sa biomasse, ses assemblages en espèces, et sa structure en taille, fait du zooplancton un bio-indicateur peu sensible des perturbations de bassins versants, particulièrement celles associées aux coupes. Ainsi, bien que l'environnement chimique et phytoplanctonique des lacs aux bassins versants coupés ou brûlés différait de celui des des lacs de référence (Carignan, D'Arcy & Lamontagne, 2000; Planas *et al.*, 2000), seuls quelques uns des nombreux attributs du zooplancton examinés ont montré une réponse notable face aux perturbations de bassins versants (Tableau I). Les attributs de structure en taille se sont révélés les plus sensibles, confirmant les propos de Sprules et Holtby (1979) selon lesquels la structure en taille des communautés zooplanctoniques reflète aussi bien, sinon mieux, les caractéristiques limnologiques des lacs que les attributs taxonomiques. Le cas des calanoïdes dont la biomasse s'est vue diminuée dans les lacs coupés et, dans une moindre mesure, dans les lacs brûlés, rejoint d'autres études rapportant la sensibilité de ces organismes face à un enrichissement en éléments nutritifs (Patalas, 1972; Pace, 1986). Nous confirmons donc ici cette caractéristique des calanoïdes comme étant un groupe taxonomique particulièrement sensible aux perturbations environnementales, notamment la coupe forestière.

Importance de la variabilité saisonnière

Une fois l'effet des coupes et des feux examiné, nous avons tenté, dans les chapitres II et III, de voir quels étaient les autres facteurs environnementaux reliés aux variations dans les assemblages d'espèces, la richesse, et la structure en taille. Dans tous les cas, moins de la moitié de la variabilité de ces attributs pouvait être reliée aux variables de concentration en éléments nutritifs, de concentration en oxygène dissous, de biovolume algal, et de densité de poisson. Ainsi, aucun des attributs du zooplancton ne semblait être fortement corrélé à son environnement, qu'il s'agisse de la condition du bassin versant ou des autres facteurs environnementaux considérés. On pourrait suggérer que le nombre de lacs étudiés (38) n'était pas assez grand pour mettre à jour les relations existantes. Ou encore, que la cinquantaine de facteurs environnementaux examinés n'incluait pas les «bons» facteurs, c'est à dire les facteurs qui influençaient réellement les communautés à l'étude (Chapitre II). Bien que ces explications soient probablement fondées en partie, elles n'amènent comme solution qu'une fuite en avant en nous incitant à échantillonner un nombre de lacs toujours plus grand et à élargir sans cesse les facteurs environnementaux à considérer.

Nous pensons qu'une partie du problème se situe ailleurs. Notre capacité à détecter des relations biologiquement significatives entre les attributs du zooplancton et les facteurs environnementaux à l'échelle du lac et de son bassin versant dépend de la précision des données de chaque lac. Or, il apparaît ici que la précision de nos données de zooplancton n'était pas assez élevée pour permettre à plus de 50% de la variabilité d'être expliquée, peu importe les facteurs environnementaux considérés. Nous croyons que ce manque de précision émane de la grande variabilité entre les mois d'échantillonnage. Ceci ne remet pas forcément en cause la validité de nos résultats. Pour augmenter la sensibilité des attributs du zooplancton face à divers facteurs environnementaux, il nous faut tout d'abord chercher à augmenter la précision des données issues de chaque lac en augmentant la fréquence d'échantillonnage. Ceci est illustré à la Figure 2 où nous voyons qu'une augmentation de la fréquence d'échantillonnage a autant d'effet qu'une augmentation du nombre de lac échantillonnés sur l'erreur associée aux modèles d'analyse de variance, du moins, tant que la fréquence d'échantillonnage ne dépasse pas cinq par lac et par été.

Dans l'ensemble, toutefois, c'est par une augmentation du nombre de lacs que la variance du terme d'erreur diminue le plus rapidement.

Hélas, une telle suggestion risque d'avoir peu d'écho, puisque peu de programmes de recherche disposent de suffisamment de ressources pour échantillonner un si grand nombre de lacs (38), un si grand nombre de fois au cours d'un été (trois fois), pendant autant d'années (trois), tout en considérant un si grand nombre de facteurs abiotiques et biotiques.

Pourtant, comment expliquer le fait que certaines études rapportent de fortes corrélations entre, par exemple, la biomasse du zooplancton et le phosphore total, alors qu'elles sont basées sur un seul échantillonnage d'une série de lacs? L'étendue statistique des variables considérées peut en partie expliquer une telle disparité. La Figure 3 montre qu'une grande étendue dans les données de concentration en phosphore (> 2,5 ordres de grandeur) va généralement de paire avec des coefficients de détermination élevés. L'effet de l'étendue statistique des variables sur la force des corrélations qui en résultent est discuté plus en profondeur dans Duarte (1991: 308). Les études de Yan (1986) et Pace (1986), quant à elles, sont basées sur une échelle de variation réduite (0,5 et 1,2 ordre de grandeur respectivement), similaire à celle de la présente étude (0,4). Pourtant, la force des corrélations rapportées par ces auteurs (r^2>60%) est supérieure à celle de la présente étude (r^2=19% pour 20 lacs de référence, Figure 1A). Mais les fréquences d'échantillonnage y étaient également plus élevées: une ou deux fois par mois dans l'étude de Yan et une fois par mois pendant cinq mois dans l'étude de Pace. Ainsi, on peut penser que la précision de leurs données de biomasse de zooplancton était plus grande et par là même, mieux corrélées aux données de phosphore total. Dans l'étude de Bays & Crisman (1983), on observe une corrélation élevée entre la biomasse du micro-zooplancton et le phosphore totale (r^2=76%) malgré une échelle de variation intermédiaire (deux ordres de grandeur) et un seul échantillonnage des lacs. Un seul échantillonnage pourrait suffire en théorie si la variabilité temporelle est faible. Or, l'étude de Bays & Crisman se situe en Floride, bien plus au sud que les études de Yan (sud de l'Ontario) et de Pace (sud du Québec). Nous suggérons que les variations temporelles de biomasse du zooplancton sont plus fortes à mesure que nous nous approchons des pôles, la saison des eaux libres étant progressivement confinée à quelques mois. Par conséquent, un échantillonnage plus intensif du zooplancton serait nécessaire pour obtenir un même degré de précision des résultats à mesure que nous nous éloignons de l'équateur. Bien que cette idée doive être examinée plus en détail, elle pourrait expliquer une partie de la variabilité des coefficients de détermination (r^2) rapportés dans la littérature, en faisant un lien entre l'étendue statistique des données, la variabilité temporelle du zooplancton et la fréquence d'échantillonnage.

Perspectives

Les conclusions de cette étude ne sont valables que si le groupe de lacs de référence représente fidèlement les groupes «Coupes» et «Feux» avant le passage des perturbations. Les trois groupes de lacs viennent de la même région géographique, géologique, climatique et présentent des valeurs comparables quant à la profondeur maximum, à l'aire de lac, et à l'aire de bassin versant, une situation plutôt favorable. Par ailleurs, l'échantillonnage des lacs présentés dans cette étude se poursuit à ce jour, et certains lacs de référence ont depuis vu leur bassins versants déboisés par la coupe forestière. Il sera intéressant de voir si ces lacs réagissent suite à la coupe. Sur la base des données présentées au chapitre I, on pourrait s'attendre à une variation – vraisemblablement à la baisse – de moins de 25% de la biomasse du zooplancton. Selon l'importance de la variabilité inter-annuelle, une telle variation sera déclarée significative ou non.

Cette thèse s'inscrit à la suite d'autres études cherchant à évaluer les impacts des perturbations environnementales sur le biota. Toutes sont confrontées au même problème de variabilité de la matière vivante – celle possiblement induite par le facteur à l'étude et celle liée au temps, à l'espace et aux gradients environnementaux. Pour ne prendre que deux exemples parmi bien d'autres de perturbations d'origine anthropique qui ont fait l'objet d'études, les effets des effluents papetiers et des pesticides sur les communautés planctoniques ont d'abord été examinés en laboratoire ou en enclos (e.g. deNoyelles, Kettle & Sinn, 1982; Holmbom & Lehtinen, 1980; Stockner & Costella, 1976; Blaise, Bermingham & van Coillie, 1985). Une telle approche écotoxicologique dérivée de la tradition pharmacologique a pour but d'établir des relations dose-réponse qui permettent de classer les organismes en fonction de leur sensibilité à une source de perturbation définie ou, inversement, de quantifier la toxicité de différents polluants par rapport à un organisme choisi. Ces études ne tiennent pas compte, toutefois, des conditions environnementales réelles du milieu qui peuvent tamponner ou exacerber les effets d'une perturbation par rapport aux résultats obtenus en laboratoire. Citons par exemple les interactions trophiques entre les espèces d'une communauté et les facteurs à grande échelle tels le climat et les saisons qui ne peuvent être reproduites en laboratoire.

Les études à grande échelle comblent cette lacune en examinant les composantes d'un écosystème telles qu'elles se retrouvent dans le milieu naturel. Elles permettent également l'étude de perturbations qui ne sauraient être reproduites en laboratoire, en l'occurrence les coupes forestières et les feux de forêt. Aussi, même s'il n'est plus possible, dans un tel contexte, de contrôler tous les facteurs qui peuvent influencer le phénomène à l'étude, nous l'abordons avec un plus grand réalisme (Carpenter, 1996; Schindler, 1998). La triste remarque de Bormann selon laquelle, bien qu'il existe de nombreux écosystèmes où les *effets* de la pollution ne peuvent toujours pas être détectés, il n'en existe plus où les *polluants* ne peuvent pas être détectés (Bormann, 1982 cité dans Schindler, 1987), devrait nous inciter à maintenir des programmes de recherche à grande échelle pour définir les effets des perturbations d'origine anthropique de plus en plus dispersés à l'échelle de la planète. Pour l'instant, nous pouvons nous réjouir de constater que les effets de la coupe forestière sur les communautés aquatiques semblent moindres que ceux occasionnés par les feux de forêt naturels. Toutefois, l'intensification de l'exploitation forestière au Canada demande que nous restions alertes et informés de l'état de santé de l'écosystème boréale face aux coupes forestières et aux autres perturbations.

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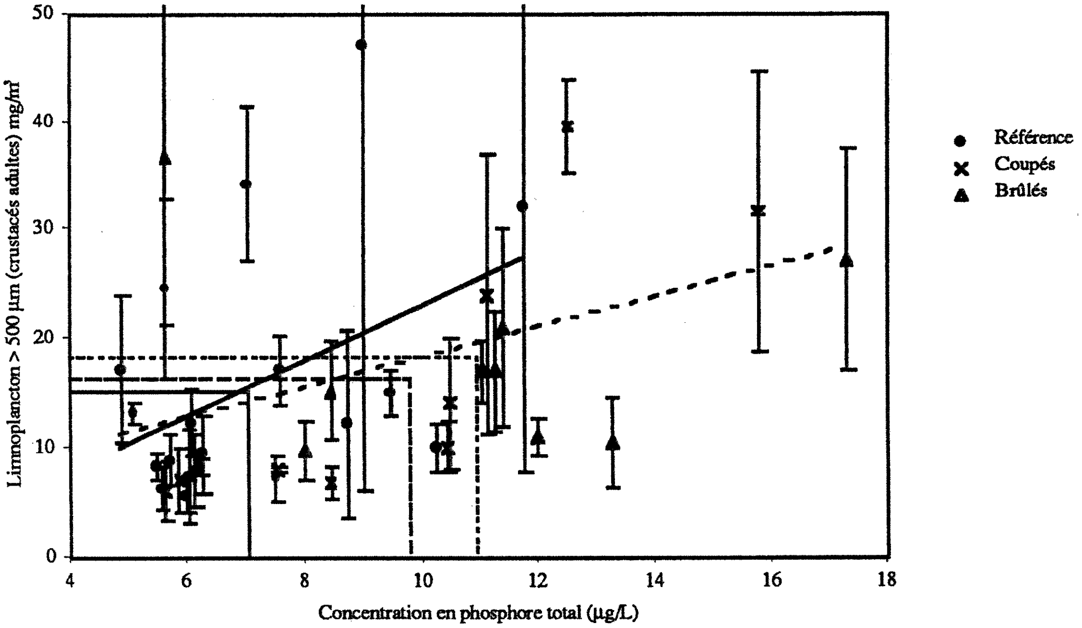
Tableau I. Résumé des différents attributs de structure des communautés zooplanctoniques examinés, en fonction des trois approches (en lignes) et des trois méthodes d'analyse (en colonnes). Un signe «–» indique que cet attribut ne s'est pas montré sensible aux coupes ou aux feux. Un signe «↑» indique que cet attribut a augmenté dans les lacs aux basins versants coupés (C) ou brûlés (F) par rapport aux lacs de référence, et inversement pour un signe «↓». Un signe entre parenthèse indique une réponse qui n'a pu être déclarée statistiquement significative (à α=5%) dans la présente étude, mais qui pourrait s'avérer vraie dans des travaux ultérieurs. Les réponses sont indiquées pour la première année après coupes et feux dans le cas des analyses taxonomiques; pour la première et deuxième années dans le cas des analyses par compteur optique de particules; pour les trois premières années dans les cas du limnoplancton (1996 / 1997 / 1998).

Approche	Variable	Analyses taxonomiques	Limnoplancton	Compteur optique de particules
Biomasse	Biomasse totale	—	— / — / —	— / —
	Biomasse des cladocères	—		
	Biomasse des calanoïdes	↓C (↓F)		
	Biomasse des cyclopoïdes	—		
	Biomasse des rotifères	(↑F)		
Composition en espèces	Composition en espèces	—		
	Richesse totale	(↑C, F)		
	Richesse des rotifères	(↑C, F)		
	Richesse des crustacés	—		
Structure ent taille	Limnoplancton 50-100 µm		— / — / —	
	Limnoplancton 100-200 µm		↑F / ↑F / —	
	Limnoplancton 200-500 µm		— / — / —	
	Limnoplancton > 500 µm		— / (↑F) / —	
	Spectres de taille			(↑C), ↑F / ↑F

Figure 1. Diagramme de dispersion de la biomasse du zooplancton (mg masse sèche sans cendres par m^3) en fonction de la concentration en phosphore totale (moyennes de l'année 1996). Les barres d'erreur représentent l'erreur type sur les trois mesures correspondant aux mois de juin, juillet et septembre. L'erreur type sur la concentration de phosphore représente en moyenne 30% de l'erreur sur la biomasse. Les moyennes de biomasse et de phosphore sont illustrées par le trait plein pour le groupe de lacs de référence; par le tiret pour le groupe de lacs coupés; par le pointillé pour le groupe de lac brûlés. A) Biomasse des grands crustacés (limnoplancton > 500 µm). Droite de régression pour les lacs de référence (droite pleine, n=20): Y = 2,6 (X) – 2,9, r^2=19%, erreur résiduelle=10.2, P=0,052. Droite de régression pour les 38 lacs (droite pointillée): Y = 1,4 (X) + 4,3; r^2=16%, erreur résiduelle=10,0 P=0.013. B) Biomasse des algues, rotifères et nauplii de calanoïdes (limnoplancton 100-200 µm). Droite de régression pour les lacs de référence (n=20): Y = 0,9 (X) + 4,9, r^2=17%, erreur résiduelle=3,8, P=0,070. Droite de régression pour les 38 lacs: Y = 1,1 (X) + 3,4, r^2=30%, erreur résiduelle=5,2, P=0.0004.

Figure 1A)


50
40
30
20
10
0
Limnoplancton > 500 µm (crustacés adultes) mg/m³
4
6
8
10
12
14
16
18
Concentration en phosphore total (µg/L)
● Référence
✖ Coupés
▲ Brûlés

B)

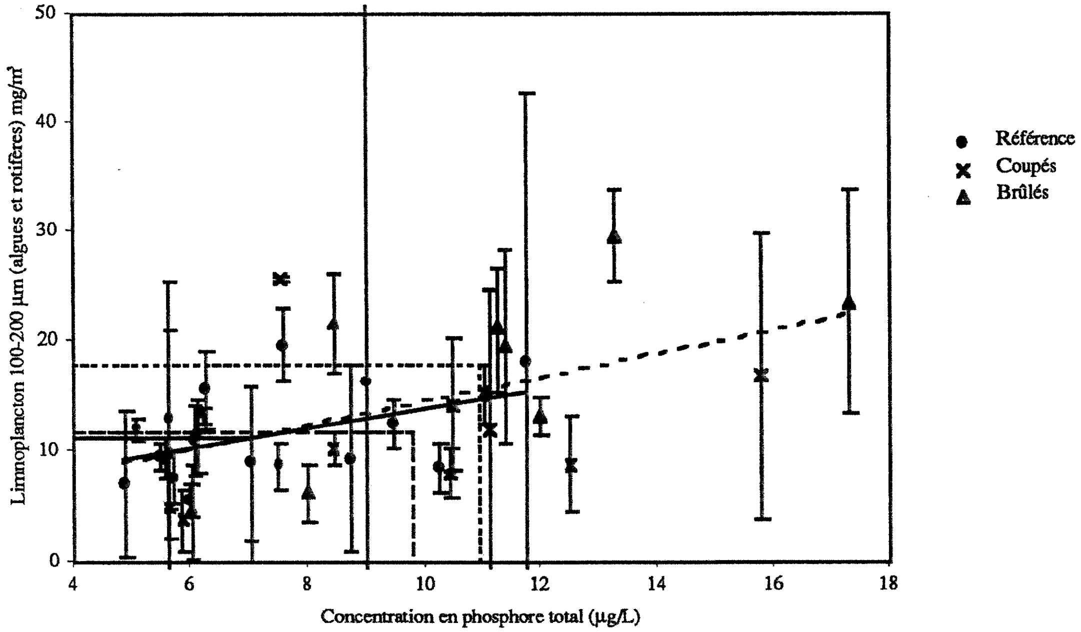

50
40
30
20
10
0
Limnoplancton 100-200 µm (algues et rotifères) mg/m³
4
6
8
10
12
14
16
18
Concentration en phosphore total (µg/L)
● Référence
✖ Coupés
▲ Brûlés

Figure 2. Analyse de répartition des ressources démontrant que pour diminuer l'erreur des modèles d'analyse de variance du biovolume des crustacés, il faut augmenter soit la fréquence d'échantillonnage (actuellement fixée à trois par année) ou augmenter le nombre de lacs échantillonnés (actuellement de 13 par groupe en moyenne). Noter qu'une augmentation de la fréquence d'échantillonnage a le même effet qu'une augmentation du nombre de lac tant que la fréquence d'échantillonnage n'excède pas cinq par lac par été. Analyse faite selon Sokal & Rohlf (1981: 309, *Optimal allocation of resources*).

Figure 2.

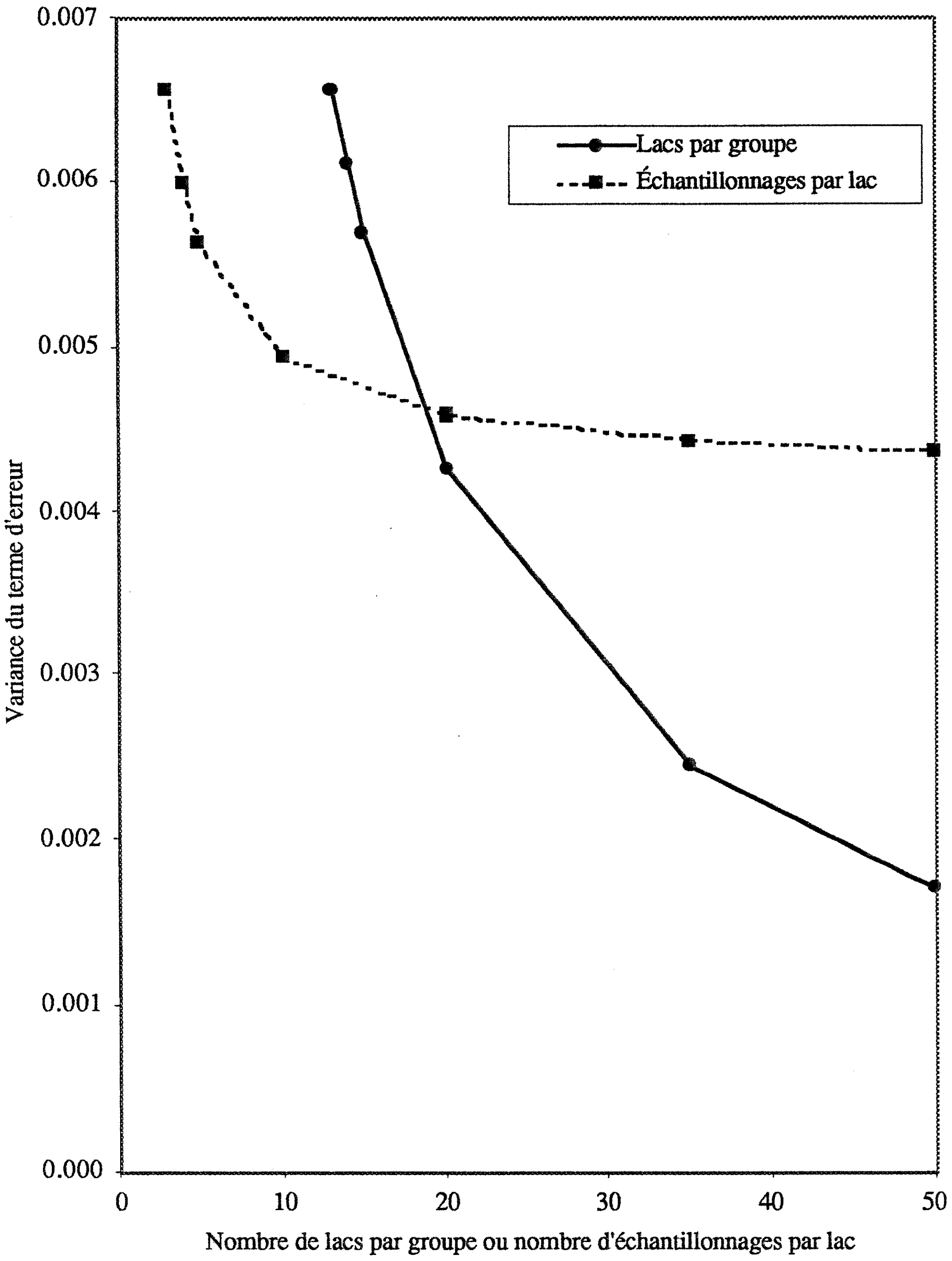
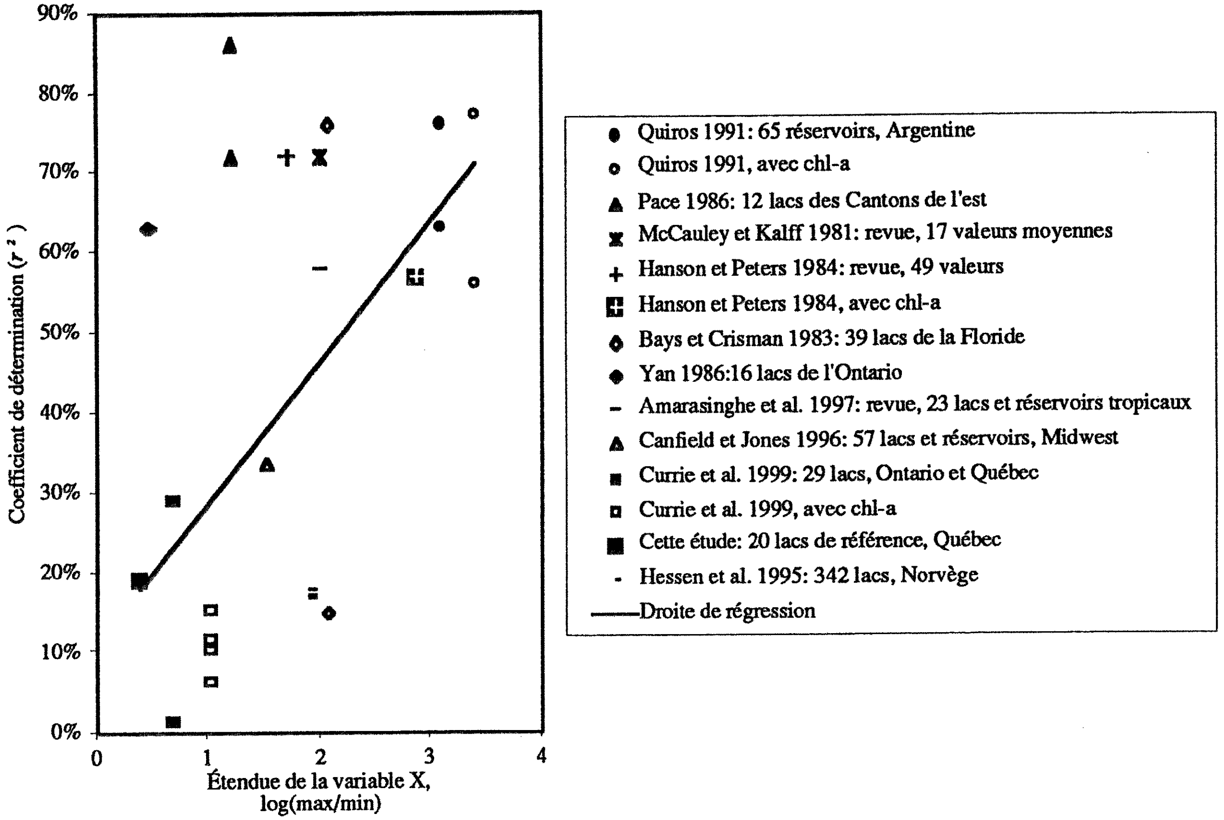

0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
Variance du terme d'erreur
0
10
20
30
40
50
Nombre de lacs par groupe ou nombre d'échantillonnages par lac
Lacs par groupe
Échantillonnages par lac

Figure 3. Diagramme de dispersion des coefficients de corrélation rapportés par divers auteurs entre la biomasse du zooplancton et la concentration en phosphore totale (ou la chlorophylle *a*) et l'étendue statistique de la concentration en phosphore (ou en chlorophylle *a*). La droite de régression suit la forme Y = 0,18(X) + 0,11; r^2=31%; erreur résiduelle: 25%; P=0,004.


90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Coefficient de détermination (r^2)
0
1
2
3
4
Étendue de la variable X,
log(max/min)
● Quiros 1991: 65 réservoirs, Argentine
○ Quiros 1991, avec chl-a
▲ Pace 1986: 12 lacs des Cantons de l'est
✖ McCauley et Kalff 1981: revue, 17 valeurs moyennes
+ Hanson et Peters 1984: revue, 49 valeurs
⊞ Hanson et Peters 1984, avec chl-a
◇ Bays et Crisman 1983: 39 lacs de la Floride
◆ Yan 1986:16 lacs de l'Ontario
– Amarasinghe et al. 1997: revue, 23 lacs et réservoirs tropicaux
△ Canfield et Jones 1996: 57 lacs et réservoirs, Midwest
■ Currie et al. 1999: 29 lacs, Ontario et Québec
□ Currie et al. 1999, avec chl-a
■ Cette étude: 20 lacs de référence, Québec
- Hessen et al. 1995: 342 lacs, Norvège
—Droite de régression

COMMENT – Effects of logging and forest fires on zooplankton biomass of Canadian Boreal Shield lakes – a revisited interpretation of results based on multiple testing

A. Patoine

In a paper about the effects of logging and forest fires on the biomass of zooplankton, Patoine et al. (2000) examined zooplankton biomass variation among three groups of Canadian Boreal Shield lakes characterised by different catchment conditions: logged, burnt, or unperturbed. They hypothesised that catchment condition was a significant source of variation in zooplankton biomass. The statistical procedure consisted in one-way, mixed-model, repeated-measure analyses of variance (RM-ANOVAs) where the response variable was the biomass of total zooplankton, the fixed treatment was catchment condition (reference, logged or burnt), and the random, repeated measures factor was month of sampling (June, July or September). The hypothesis was tested for one, two, and three years following the passage of logging activities and forest fires, and for different taxonomic and size-based sub-groups of total zooplankton. Twenty (20) tests were performed in all, presented in Table 2 of the paper. The null hypothesis of no effect was rejected in three cases out of 20, using, for each test, a risk level for type I error of $\alpha=5\%$. These cases were for calanoids one year after perturbations ($P=0.01$), and for the 100-200 μm size fraction of limnoplankton (mostly rotifers, nauplii and algae), one ($P=0.030$), and two ($P=0.020$) years after perturbations. Based on these results, the authors concluded that among-group variations in these three biomass variables were statistically significant, at the $\alpha=5\%$ level, and went on to perform post-hoc Scheffe multiple range tests to assess which pairs represent different groups of lakes.

Such a procedure did not take into account the increased overall probability of making a type I error i.e. of incorrectly rejecting the hypothesis of no effect (Pierre

Legendre, personal communication). For randomly generated data, there is a probability of 0.64 of rejecting the null hypothesis at least once over 20 tests, at the nominal $\alpha=0.05$ level. The value of 0.64 is obtained from the binomial distribution: $P= 1-(0.95)^{20}$. It is therefore important to take into account the increase in the overall probability of type I error when reading the individual probability values presented in Table 2 in Patoine et al. (2000). Methods for calculating adjusted levels of significance vary depending on whether the multiple tests represent independent or non-independent tests. In the present case, the data on which analyses were performed all came from the same series of lakes, so we present here an application of Holm's procedure for non-independent tests (Holm, 1979 cited in Legendre and Legendre 1998: 18). The test requires that 1- the probability values be listed in such a way that $p_1 \leq p_2 \leq ... \leq p_i \leq ... \leq p_k$; 2- an adjusted probability p_i value be calculated such that $p'_i=p_i(k-i+1)$; 3- p'_i be made equal to p'_{i-1} if $p'_i<p'_{i-1}$; 4- each adjusted p'_i be compared to the unadjusted α significance level. According to this procedure, the null hypothesis of no among-group variation in zooplankton biomass is accepted in all 20 cases (Table 1). Hence, some claims in the paper by Patoine et al. (2000) should be revised. In particular, the following statement is false: "Our hypothesis of greater zooplankton biomass in disturbed-watershed lakes was supported in the case of burned-watershed lakes but not in the case of logged-watershed lakes" (p. 161). The statistical evidence does not allow us to reject the hypothesis of no effect of catchment logging or burning on zooplankton biomass. We therefore cannot conclude that the observed biomass variation among the groups of lakes represents an effect of catchment perturbations, neither by logging, nor burning. If these biomass variations did represent a true effect of catchment perturbations, however, the study design would have had a probability of 50% at most of detecting it, as power analysis had demonstrated in the original paper. The most that can be concluded, therefore, is that, if catchment perturbations have an effect on zooplankton biomass, the effect is less than a 50%

variation relative to reference lakes (less than 100% in the case of the 100-200 μm size fraction of limnoplankton), and is generally greater in the case of fires than in the case of logging (Patoine et al. 2000).

There was, nonetheless, a recurring pattern of greater average biomass values in burnt-catchment lakes relative to reference lakes, found in all of the four size fractions during the first two years following catchment perturbations. One might argue that such a recurring pattern would be unlikely in randomly generated data, and could therefore suggest a tendency towards greater limnoplankton biomass in burnt lakes relative to reference lakes. Since the four size fractions are obtained through sequential filtration of an original sample ("total limnoplankton"), however, they are not entirely independent measurements. It may therefore be expected that the among-group variation in each size fraction follow a similar pattern.

A posteriori corrections of probability values tend to be overly conservative and are therefore not the best way to test hypotheses. One should rather seek to perform, from the beginning, one single statistical test that takes into account all dependent and independent variables of interest (Pierre Legendre, personal communication). In the present case, a single redundancy analysis (RDA) could have been performed with the four size fractions of limnoplankton as the dependent matrix, and an independent matrix of dummy variables coding for two factors and their interaction: catchment condition and year. Significance testing of the trace (variance of the dependent matrix explained by the independent matrix) by random row permutation would then allow to determine if one or more factors included in the model (catchment condition, year, or catchment-year interaction) represent significant sources of variation. The inclusion of an interaction term, however, supposes a balanced design whereby all combinations of catchment condition with year contain the same number of observations, which is not the case here. We therefore present the results of an RDA performed on the 1996 (one year after perturbations) limnoplankton biomass data, with catchment condition as the independent variable. The analysis was performed on log(x+1) transformed values of limnoplankton biomass (mg ash-free dry mass•m^{-3}) in four size fractions: 50-100 µm (mostly algae and rotifers), 100-200 (rotifers, nauplii, algae), 200-500 µm (small or immature crustaceans), and > 500 µm (large or adult crustaceans). The dependent matrix used in the analysis consisted in 114 rows representing the 38 lakes sampled three times during summer 1996 (one year after perturbations) and four columns representing log(x+1)-transformed biomass values of the four limnoplankton size fractions. The independent matrix consisted in 114 rows and two columns of binary variables coding for reference lakes (1, 0), logged-catchment lakes (0, 1), and burnt-catchment lakes (0, 0). To control for the repeated sampling of the 38 lakes, a covariable file was also included in the analysis that coded for date of sampling: June (1, 0), July (0, 1), or September (0, 0). The total amount of variation in the limnoplankton data set that was explained by catchment condition was tested for statistical significance by 999 random row permutations conditioned on sampling date. The analysis is thus equivalent to a repeated-measure multivariate analysis of variance, with the added advantage that environment-limnoplankton ordination biplot may be obtained. The analysis was performed with Canoco version 3.11 for Macintosh.

The amount of variation in limnoplankton biomass size structure that could be explained by catchment condition was low (5.8%) and non-significant at the α=5% level (*P*=0.057). Among the four size fractions, the 100-200 µm one presented the greatest amount of among-group variation, as shown by the length of the projection of the 100-200 µm vector on canonical axis I (Figure 1). Projections of the burnt centroid and the reference centroid at right angle on the 100-200 µm size vector show that burnt-catchment lakes tended to have higher biomass values of this size fraction than reference lakes. In short, results are qualitatively very much like those presented in Patoine et al. (2000) for limnoplankton, one year after perturbations. Although the probability value of 0.057 does not lead us to reject the hypothesis of no effect, it is sufficiently close to the significance level of 0.05 to warrant us of possible effects of wildfires on limnoplankton biomass, especially on the rotifer-nauplii-algae size fraction.

It is reassuring to see that an alternative statistical procedure to the analysis of limnoplankton biomass in perturbed- and unperturbed-catchment lakes leads to conclusions similar to those presented in Patoine et al. (2000). We cannot conclude that logging or wildfires have an effect on limnoplankton size structure. As demonstrated in Patoine et al. (2000), however, the high among-lake and among-month variability of limnoplankton biomass within reference lakes results in low (<50%) statistical power. This means that the inability to reject the null hypothesis of no effect could be due to an insufficient number of observations (lakes or sampling dates) rather than to a true absence of effect. The necessity of sampling a great number of lakes (no less than 20 per group) to obtain an estimate of mean zooplankton biomass that is reliable enough to detect differences (smaller than 100%) among different groups of lakes should help in deciding what environmental variables to include or not to include in future large-scale studies of the effects of catchment perturbations on aquatic ecosystems of the Canadian Boreal Shield.

References

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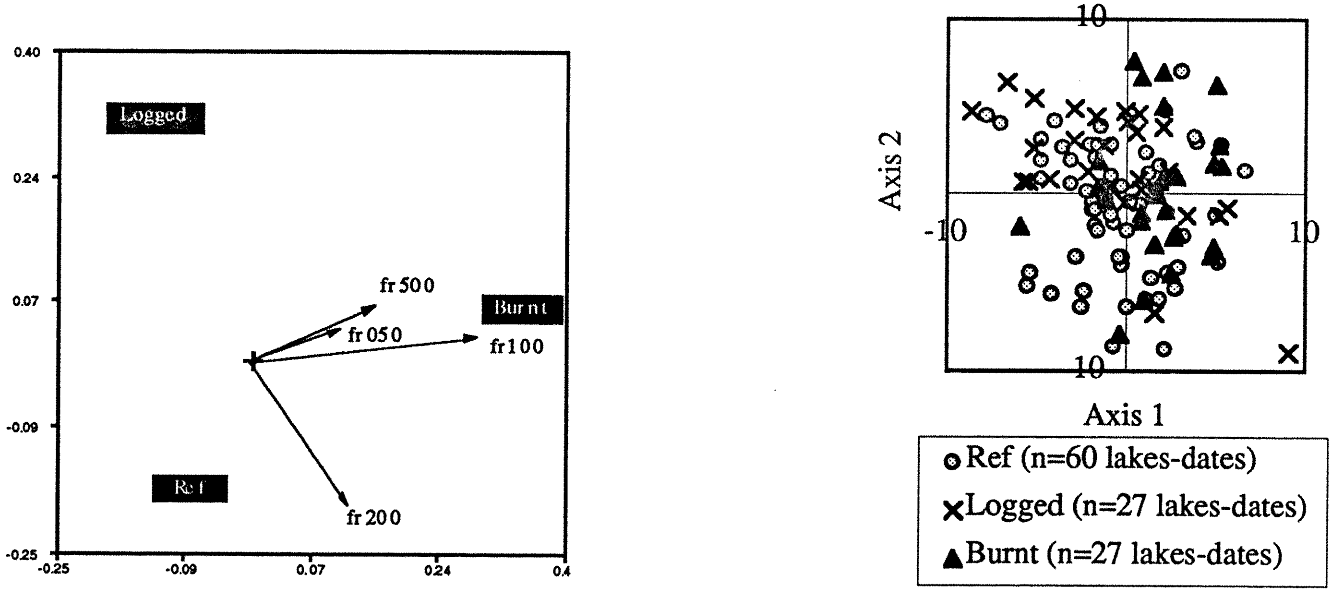
Table 5. Correction of the probability values presented in Table 2 of Patoine et al. (2000) following Holm's procedure. Probability values are from *F*-tests conducted on total zooplankton biomass and the biomass of different taxonomic-based or size-based subgroups from 38 Canadian Boreal Shield lakes divided into three groups: logged-catchment lakes (n=9), burnt-catchment lakes (n=9) and unperturbed-catchment lakes (n=20). An adjusted Holm's probability value (last column) greater than 0.05 leads to the non-rejection of the null hypothesis of no effect of catchment condition on zooplankton biomass.

Variable	Year	Original probability value	Rank	p'_i, step 3	p'_i, step 4
Calanoids	'96	0.01	1	0.20	
100 µm	'97	0.02	2	0.38	
100 µm	'96	0.03	3	0.54	
Total limno	'97	0.08	4	1.36	
500 µm	'97	0.08	5	1.28	1.36
Rotifers	'96	0.09	6	1.35	1.36
Total limno.	'96	0.11	7	1.54	
200 µm	'96	0.15	8	1.95	
Total zoopl.	'96	0.27	9	3.24	
500 µm	'96	0.29	10	3.19	
200 µm	'98	0.37	11	3.70	
050 µm	'96	0.41	12	3.69	3.70
200 µm	'97	0.47	13	3.76	
Cyclopoids	'96	0.51	14	3.57	3.76
Cladocerans	'96	0.56	15	3.36	3.76
050 µm	'98	0.56	16	2.80	3.76
100 µm	'98	0.68	17	2.72	3.76
050 µm	'97	0.78	18	2.34	3.76
Total limno	'98	0.85	19	1.70	3.76
500 µm	'98	0.94	20	0.94	3.76

Figure 1. Correlation biplot in species-environment space (A) and sample space (B) representing limnoplankton biomass variations in four size fractions among three groups of lakes characterized by different catchment condition: logged (nine lakes sampled three times), burnt (nine lakes sampled three times) or unperturbed (reference, 20 lakes sampled three times). Sum of all eigenvalues after fitting time of sampling: 0.798. Sum of all canonical eigenvalues: 0.046 (or 5.8%, *P*=0.057, 999 permutations conditioned on time of sampling). Eigenvalues of canonical axes I and II: 0.035 (or 4.4%, *P*=0.11); 0.011 (or 1.4%, *P*=0.36).



A)

B)