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Comparative Impact of Natural Fires and Forest Logging on Zooplankton Communities of Boreal Lakes

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by

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ABSTRACT

The goal of the research project was to determine if natural fires and forest logging have a significant impact on zooplankton biomass, biodiversity, species assemblages, and size spectra in lakes of the Canadian Boreal Shield. Wildfires and logging disturbances occurred in 1995. The research project was carried out from 1996 to 1998 in 38 lakes of the boreal forest in Québec: Twenty (20) lakes, undisturbed since 70 years, served as references; nine (9) lakes had 9-72% of their watershed logged and another 9 lakes had 50-100% of their watershed burnt. Three methodological approaches were used to determine zooplankton attributes: a) taxonomic analysis for zooplankton biomass, species richness and assemblages, b) analysis of size-fractionated limnoplankton ash-free dry weight, and c) determination of crustacean biovolume size spectra using an Optical Particle Counter (OPC). Our study reveals that natural fire and logging disturbances have different impacts on zooplankton community of boreal lakes. Natural fires increase zooplankton and limnoplankton biomass because of higher inputs of mineral nutrients (nitrates and phosphorus) from burnt watersheds. Burnt lakes supported on average 53-64% more biomass of cyclopoids and rotifers (or 59% more biomass of limnoplankton 100-200 μm size fraction) than reference lakes the first 2 years after fire. In contrast, logging does not increase zooplankton biomass because of higher inputs of dissolved organic carbon from watershed which inhibit light transmission and biological production. Cut lakes supported on average 43% fewer biomass of calanoids than reference lakes during the first year after logging. The biomass of cladocerans and copepodite stages did not vary significantly among reference, cut and burnt lakes. The impacts of natural fire and logging on zooplankton biomass were more pronounced 2 years after disturbances. Impacts of wildfire and logging on zooplankton biodiversity and species assemblages, measured the first year following disturbances, are minor. Crustacean biovolumes in large size classes (1200-1500 μm) were higher in perturbed lakes, especially in burnt lakes. Zooplankton biomass and size spectra, as well as limnoplankton biomass are promising tools to monitor the effects of watershed disturbances by natural fire and logging on zooplankton communities in boreal lakes. However among-lake and seasonal changes in watershed and limnological characteristics are more important sources of variability in zooplankton biomass than watershed disturbances, and should be considered when assessing the environmental impacts of watershed disturbances on zooplankton in boreal lakes .

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INTRODUCTION

Logging and natural fires are common disturbances of the Canadian boreal forest (Dansereau and Bergeron 1993; Natural Resources Canada 1996). New strategies in forest management are based on the assumption that emulating natural disturbances such as wildfires in logging practices will sustain forest dynamics and biodiversity (Hunter 1993). Such strategies, however, were developed without considering aquatic ecosystems which are expressive and abundant features of boreal forest landscapes. Comparing the impacts of wildfires and logging on aquatic ecosystems is a necessary step towards forest management practices that take into account the global impacts of logging on water quality and aquatic biota of forested lakes and streams.

Relatively few studies have documented and compared the effects of wildfires and logging on chemistry and biology of boreal lakes. Most studies were carried out in streams and reported increases in concentrations of particulate organic matter, phosphorus, nitrogen and ions after forest fires (Bayley et al. 1992) and clear-cutting (Likens et al. 1970; Nicholson et al. 1982). Assessment of changes in stream biota following watershed disturbances gave conflicting results. The biomass of macroinvertebrate communities has been shown to increase in some streams (Burton and Ulrich 1994) but not in others (Minshall et al. 1997). The comparative effects of wildfires and logging on lake biology are much less known relative to effects on stream biology. In some cases, logging was associated with increases in algal biomass (chlorophyll *a*) 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 in chlorophyll *a*, total phosphorus and nitrogen, and dissolved organic carbon concentrations between logged and reference lakes were undetectable (Lehmann 1994).

A recent project carried out from 1995 to 1998 in Québec under the SFM Network of Excellence provided the first and unique opportunity to compare and model the impacts of fire and forest harvesting on water quality and biota in Boreal Shield lakes (Carignan et al. 1999). The main scientific publications resulting from this research program will be published on a special issue of the Canadian Journal of Fisheries and Aquatic Science in 2000. Studies reported on the comparative impacts of forest fire and harvesting on water quality (Carignan et al. 2000), runoff and element export from catchments (Lamontagne et al. 2000), pelagic and benthic algal biomass (Planas et al. 2000), zooplankton and limnoplankton biomass (Patoine et al. 2000a) and fish communities (St-Onge and Magnan 2000).

Zooplankton is an essential component of lake biota: by grazing on the phytoplankton community, zooplankton can control algal biomass and size structure (Christoffersen et al. 1993) as well as phosphorus-chlorophyll *a* relationships (Mazumder 1994; Pace 1984), contribute to nutrient recycling (Lehman 1980), and increase water transparency (Lampert et al. 1986) and mixing depth (Mazumder et al. 1990). Zooplankton biomass in Canadian Boreal Shield lakes is positively related to the concentrations of nutrients (TP and TN) (Yan 1986). As nutrient inputs from watersheds significantly increase after deforestation (Carignan et al. 1999), this enrichment is susceptible to affect bottom-up interactions and plankton (phyto- and zooplankton). It is therefore likely, but yet unknown, that zooplankton biomass in logged and burnt lakes should be somewhat higher than in unperturbed reference lakes. Direct effects of logging or fires on fish communities, as reported for brook trout (Berubé and Lévesque 1995), may also indirectly influence zooplankton biomass and size structure. Furthermore, as fish yield and recruitment is strongly correlated to lake productivity and plankton food availability (Godbout and Peters 1988), any changes in zooplankton resources may thereafter impact sportfish populations.

The present study is the first to compare the effects of natural forest fires and clear-cut logging on different attributes of zooplankton communities in Canadian Boreal Shield lakes. We present the results of three years of zooplankton survey in 38 lakes of central Québec characterised by different watershed conditions: reference, cut and burnt. We predict that zooplankton and limnoplankton biomass will be higher in cut and burnt lakes than in reference lakes. We also assessed the comparative effects of natural fire and logging on zooplankton biodiversity and species assemblages at short term (first year after disturbances), and on crustacean biovolume and size spectra (first 2 years after disturbances). The relative influence of natural sources of variation (within- and among-lake, sampling months and years) and watershed conditions (reference, cut, burnt) on zooplankton attributes were evaluated, as well as the relationships between zooplankton community attributes and the intensity of disturbances, and lake environmental characteristics (water chemistry, nutrients, organic matter, and planktivory pressure). Preliminary results of the research are presented in Pinel-Alloul et al. (1998) and Patoine et al. (2000a).

STUDY SITE

The data were collected in 38 headwater lakes on the Boreal Canadian Shield. All the lakes are located within a 30 000-km² area around Gouin reservoir in Québec (48°50'N, 75°00'W, Fig.1). This region has a typical temperate climate, where snow represents half of the annual precipitation (900-1000 mm). Mean annual runoff varied from 490 to 694 mm during the 3-year survey; runoff was high in 1997 and low in 1998 compared with its long-term average of

586 mm (Lamontagne et al. 2000). The forest is primarily composed of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), jack pine (*Pinus divaricata*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). The lakes were chosen according to three types of watershed conditions: 20 reference lakes with undisturbed watersheds (old-growth forest of at least 70 years); 9 “logged or cut” lakes, whose watersheds had undergone forest clear-cutting over 8 to 73% of their area, and 9 “burnt” lakes, whose watersheds had been severely burned by natural fires over 50 to 100% of their area (Fig.1). In logged lakes, a buffer strip of about 20 m had generally been left between cutting zones and lakes. Most fires and clear-cuts occurred in 1995 (with the exception of lakes C24 and C2, which had been clear-cut in spring and summer 1994 respectively). Among the reference lakes chosen in 1996, four lakes had 5- to 24% of their catchment logged in winter 1996 or 1997. The lakes were selected on the basis of comparable size, basin morphometry, and catchment properties (Table 1). All the lakes were stratified during summer and their watershed slope ranged from 7.5 to 19.5% (mean = 11.1%). More details on lake selection, bedrock geology, landscape features, climate and vegetation are presented in Garcia and Carignan (1999) and Carignan et al. (2000).

Figure 1. Location of study lakes. Letters N and P before lake numbers refer to reference lakes (stars), C refers to cut lakes (circles), and F to burnt lakes (diamonds).

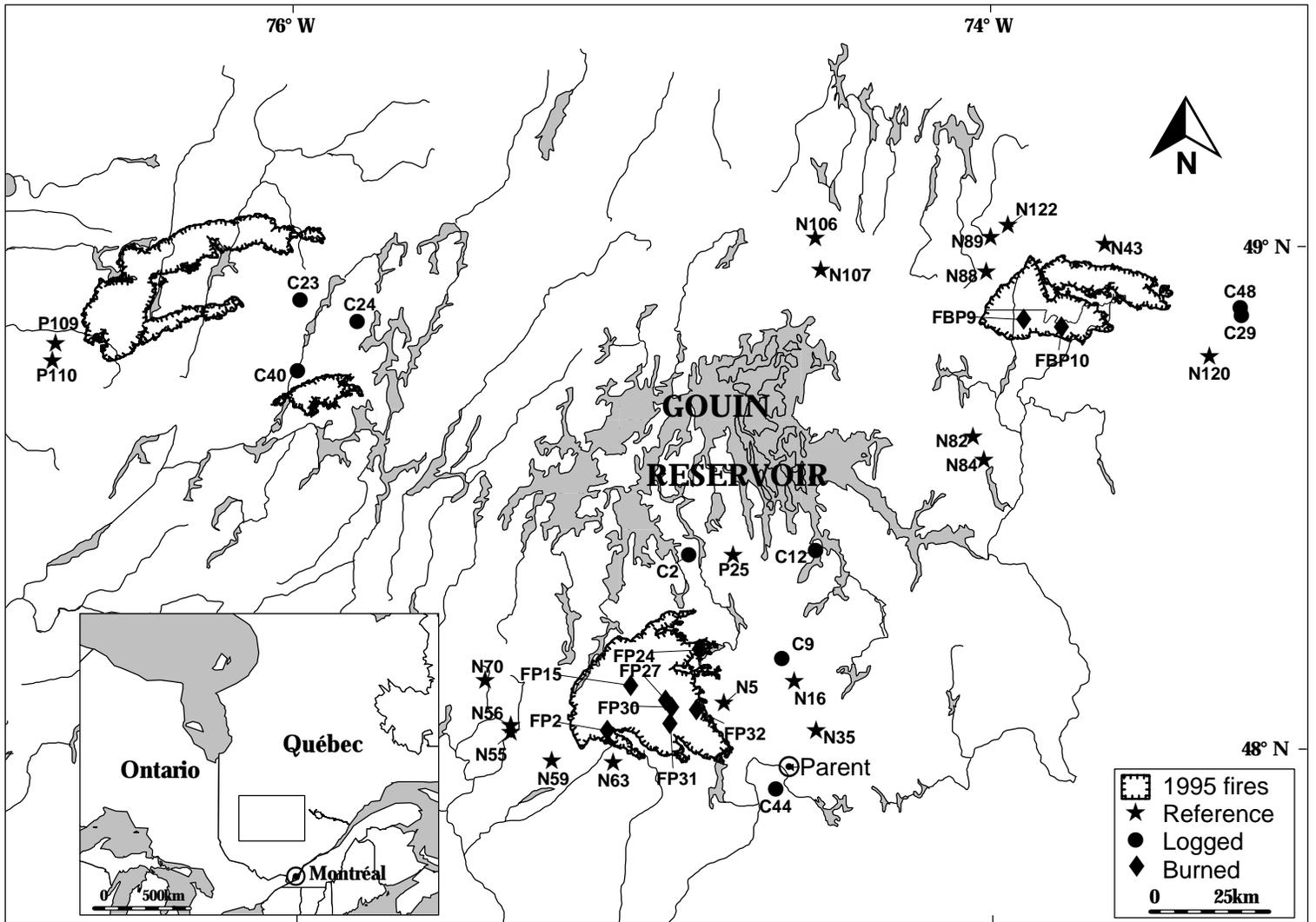


Table 1. Characteristics of the 38 lakes and their watersheds for the three groups of watershed conditions. Mean (and ranges) values are based on three years of sampling for chemical variables (1996, 1997 and 1998) and two years for chaoborids (1996 and 1997). Fish abundances were based on catches in 1996 (17 lakes) and 1997 (21 lakes)

	Reference (n = 20)	Cut (n = 9)	Burnt (n = 9)
Maximum Depth (m)	12 (7-23)	14 (5-30)	15 (10-20)†
Lake Area (ha)	44 (14-81)	34‡ (18-66‡)	40 (17-64)
Drainage Ratio	5.4 (2.3-15.4)	6.7 (2.0–13.2)	7.1 (2.5–11.6)
% Watershed Area deforested	0%	44% (7%-96%)	90% (50%-100%)
PH	6.3 (5.8–7.0)	6.1 (5.7–7.0)	6.3 (5.6–7.2)
TP ($\mu\text{g}\cdot\text{L}^{-1}$)	6.9 (4.5–11.8)	9.5 (5.4–17.3)	11.8 (5.6–17.3)
TN ($\mu\text{g}\cdot\text{L}^{-1}$)	213 (118–332)	252 (160–386)	310 (169–747)
K+ ($\mu\text{g}\cdot\text{L}^{-1}$)	232 (64–516)	521 (174–957)	754 (522–1152)
DOC ($\text{mg}\cdot\text{L}^{-1}$)	5.1 (2.5–9.1)	7.5 (2.7–13.2)	6.0 (3.0–9.3)
Chlorophyll <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	1.7 (0.8–3.4)	2.0 (1.0–3.3)	3.1 (1.2–5.2)
Chaoborids ($\text{ind}\cdot\text{m}^{-3}$)	27 (0–478)	39 (0–400)	38 (0–182)
Planktivores (CPUE)	38 (0.3-206)	26 (8–106)	36 (0.1–128)
Piscivores (CPUE)	2.8 (0–16)	3.1 (0–9.3)	4.7 (0–13.6)

† Excluding FP27: Max. Depth = 34 m

‡ Excluding C48: Lake Area = 231 ha

SUMMARY OF METHODS AND DATA ANALYSES

Detailed information on sampling design, field methods, laboratory procedures and statistical analyses used by co-researchers in the Québec project (SFM Network of Excellence) can be found in Pinel-Alloul et al. (1998), Carignan et al. (1999), Garcia and Carignan (1999), Carignan et al. (2000), Planas et al. (2000), Patoine et al. (2000a) and St Onge and Magnan (2000). Therefore, only a brief summary of methods used to study zooplankton responses to wildfires and logging is presented here.

Field Sampling

The lakes were accessed by hydroplane and sampling was done from the float. The lakes were sampled three times per year, in May-June, July and September of 1996, 1997 and 1998. All 38 lakes were sampled within a 5-days period, between 6:00 and 15:00. Water temperature and dissolved oxygen profiles were established at 0.5-m intervals with an electronic temperature/oxygen meter. Light attenuation and Secchi depth were also measured. Nutrient (TP, TN, NO₃, NH₄) dissolved organic carbon (DOC), chlorophyll *a* (Chl-*a*), and ions (K, Ca, Mg, Cl, SO₄) concentrations were estimated in the euphotic zone (see Carignan et al. 2000, and Planas et al. 2000 for details on water chemistry and pelagic phytoplankton analysis). Zooplankton was sampled in triplicates at the deepest point of the lakes by vertical tows 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 was narcotised in the field with carbonated water and preserved in 4% formaldehyde. Fish collection and analysis are described in St-Onge and Magnan (2000).

Zooplankton analysis¹

In the laboratory, zooplankton samples were examined under a stereoscopic microscope to remove Chaoborus larvae which abundance was estimated. Thereafter, zooplankton samples were split into four equal fractions with a Folsom splitter. The first quarter was used for taxonomic analysis; the second quarter was used for size fractionation and organic mass determination of limnoplankton; the third quarter was used to estimate crustacean biovolume and size spectra; the fourth quarters were kept for later studies and reference material.

¹ Taxonomic analysis of the zooplankton samples collected during the second (1997) and third (1998) years of the study is in completion.

Taxonomic analyses were performed on 10 ml sub-samples of the 1996 samples. Zooplankton was identified to species, by following the keys of Edmonson (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 each species, four taxonomic groups (cladocerans, calanoids, cyclopoids and rotifers) and total zooplankton biomass. Zooplankton biomass was expressed in mg dry weight per cubic meter. Based on abundances of each species, we determined species assemblages for the 38 lakes and the 3 months of sampling in 1996. Species with less than 5% of occurrence were excluded from the analysis. As the result, the final species matrix consisted of 62 zooplankton species. More details on taxonomic analysis are presented in Patoine et al. (2000a) and Patoine et al. (2000b).

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 $> 500 \mu\text{m}$. 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, combusted at 500°C for 18 hours and weighed again. Limnoplankton organic mass for each size fraction was calculated as the difference between the two weight measurements and expressed in mg of ash-free dry weight (AFDW) per cubic meter. Total limnoplankton biomass is the sum of the biomass of the four size fractions. Species composition of each limnoplankton size fraction was determined under 20X magnification prior to drying. The $> 500 \mu\text{m}$ 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, the $> 500 \mu\text{m}$ 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 bosminidae (6%); it will be referred to as the copepodite and small cladoceran 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 algae size fractions respectively. For more details on limnoplankton analysis, see Patoine et al (2000a).

The lab version of the Optical Plankton Counter (OPC-1L, Focal technologies, Darmouth, Nova-Scotia, Canada) was used to determine crustacean biovolume and size spectra (Herman, 1988). Plankton particle sizes were distributed in 100 μm equivalent spherical diameter (ESD)

size classes and transformed into biovolume ($\text{vol} = \text{ESD}^3/6$). Only particles of size $> 200 \mu\text{m}$ were detected by the OPC which eliminated most of rotifers. Thus, size spectra representing biovolume of crustaceans on the Y axis (mm^3/m^3 , $\log(x+1)$) and size class on the X axis (200 to 3000 μm , 100 μm increments) were constructed for each zooplankton sample. Size classes occurring in 5% or less of the lakes were eliminated. As a result, crustacean size spectra presented 22 size classes from 200-300 μm to 2300-2400 μm . Total crustacean biovolume corresponded to the sum of the biovolumes of the 22 size classes. More details on the OPC system and size spectra analysis can be found in Patoine et al. (2000c, in preparation).

Statistical analyses

We tested for statistically significant differences in zooplankton and limnoplankton attributes among reference, cut and burnt lakes. First, one-way analysis of variance (ANOVA: Sokal and Roff 1981) was performed on seasonal mean biomass values of total zooplankton, cladoceran, calanoid, cyclopoid and rotifer dry mass (1996) and for the seasonal mean biomass values of total limnoplankton and each of the four size fractions (1996, 1997 and 1998). Same analysis was performed to detect differences in zooplankton species richness and Shannon diversity index (1996), and in crustacean biovolumes (1996, 1997). 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 fall of 1996 or winter 1997. Where F tests revealed a significant treatment effect ($\alpha = 0.05$), the Duncan multiple range test was performed to assess where differences lay (SAS Institute Inc. 1988). Nested ANOVA was also performed on mean biomass values of limnoplankton and zooplankton variables to estimate the relative importance of different sources of variations (replicates, lakes, months, and watershed conditions).

Canonical Correspondence Analyses (CCA: ter Braak 1986, and partial CCA: Borcard et al. 1992) were performed to compare zooplankton species assemblages in the three groups of lakes and determine the different sources of variation (watershed conditions, months and years). Watershed conditions (reference, cut, burnt), sampling months and years were coded as binary variables and treated as co-variables. The significance testing of CCAs was performed by Monte Carlo permutations (999, $\alpha = 0.05$) (Legendre and Legendre 1998). We also used Principal Component Analysis (PCA, Legendre and Legendre 1998) to describe the overall variation in environmental factors and crustacean size spectra. To test the relative effects of the different sources of variation on crustacean size spectra, we performed ANOVA on PCA sample scores with four random nested factors: i) watershed conditions, ii) lake, iii) month, iv) year. PCA and

CCA were performed with the R package (Casgrain et al. 2000) and the JUMP statistical package (version 3, SAS Institute INC.1988) was used to perform ANOVA.

Relationships between zooplankton attributes and environmental variables were quantified by Pearson correlation or regression analysis with forward selection procedures (Sokal and Roff 1981), and Redundancy Analysis (RDA: ter Braak 1988). Environmental variables were grouped into three categories: water quality, predation and morphometry and represented bottom-up and top-down factors (McQueen et al. 1989; Pinel-Alloul et al. 1998). The bottom-up variables included pH, TP, TN, TN/TP ratio, NO₃, NH₄, DOC, K, Ca, Mg, Cl, Na, SO₄, chlorophyll a (Chl-a), and Chl-a/TP ratio. The top-down variables included the density of *Chaoborus* larva (ind./m³), the density of planktivorous fish and the density of piscivorous fish (St-Onge and Magnan 2000). Planktivorous fish included, in decreasing order of occurrence: yellow perch (*Perca flavescens*), pearl dace (*Semotilus margarita*), white sucker (*Catostomus commersoni*), golden shiner (*Notemigonus crysoleucas*), lake chub (*Couesius plumbeus*), lake whitefish (*Coregonus clupeaformis*), finescale dace (*Chrosomus neogaeus*), fallfish (*Semotilus corporalis*), and various cyprinids. Piscivorous fish included, in decreasing order of occurrence: walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), and brook trout (*Salvelinus fontinalis*). The morphometry category included drainage ratio (DR) and the proportion of the catchment area deforested by logging or forest fires (Table 1).

All statistical analyses were performed on log-transformed values ($x + 1$) or square root-transformed values to make the variables equivariant among groups of lakes (ANOVA tests) and to make the relationships linear (Pearson correlations, regression analyses).

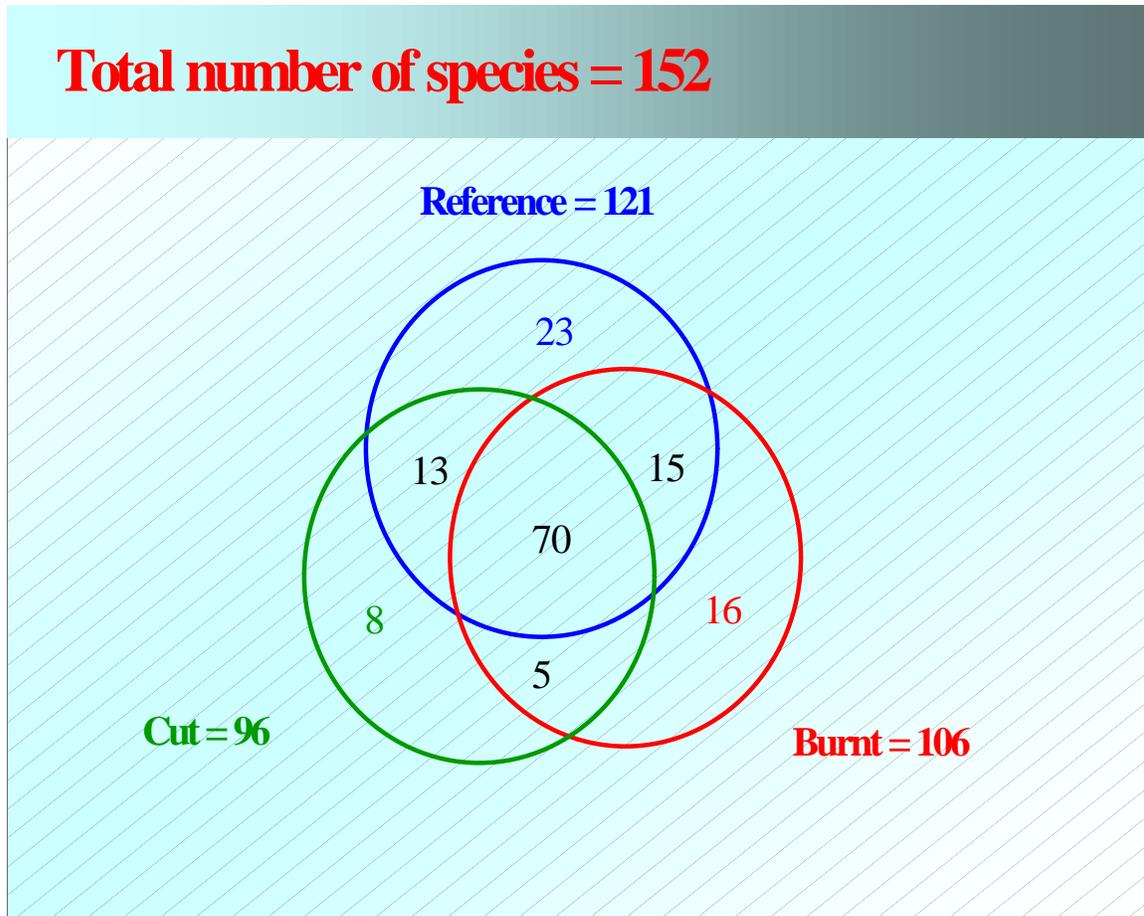
SUMMARY OF RESULTS AND DISCUSSION

Zooplankton Species Assemblages and Diversity

A total of 152 zooplankton species were identified in 1996 in the 38 lakes (Fig. 2). Almost half (46%) of the species were common to the three groups of lakes (reference, cut, 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 contains more lakes. The most frequent and ubiquitous species were the rotifers *Keratella cochlearis*, *Kellicottia longispina*, *Conochilus unicornis*, *Polyarthra vulgaris*, *P. remata*, *P. major*, *Conochiloides dossuarius*, *Gastropus stylifer*, *Filinia terminalis*, *Keratella crassa*, *K. taurocephala*, *Kellicottia bostoniensis*, *Trichocerca elongata*, *Ploesoma lenticulare* and *Polyarthra euryptera*. The most frequent species among Cladocera were *Bosmina* spp., *Daphnia longiremis*, *D. catawba*, *D. pulex*,

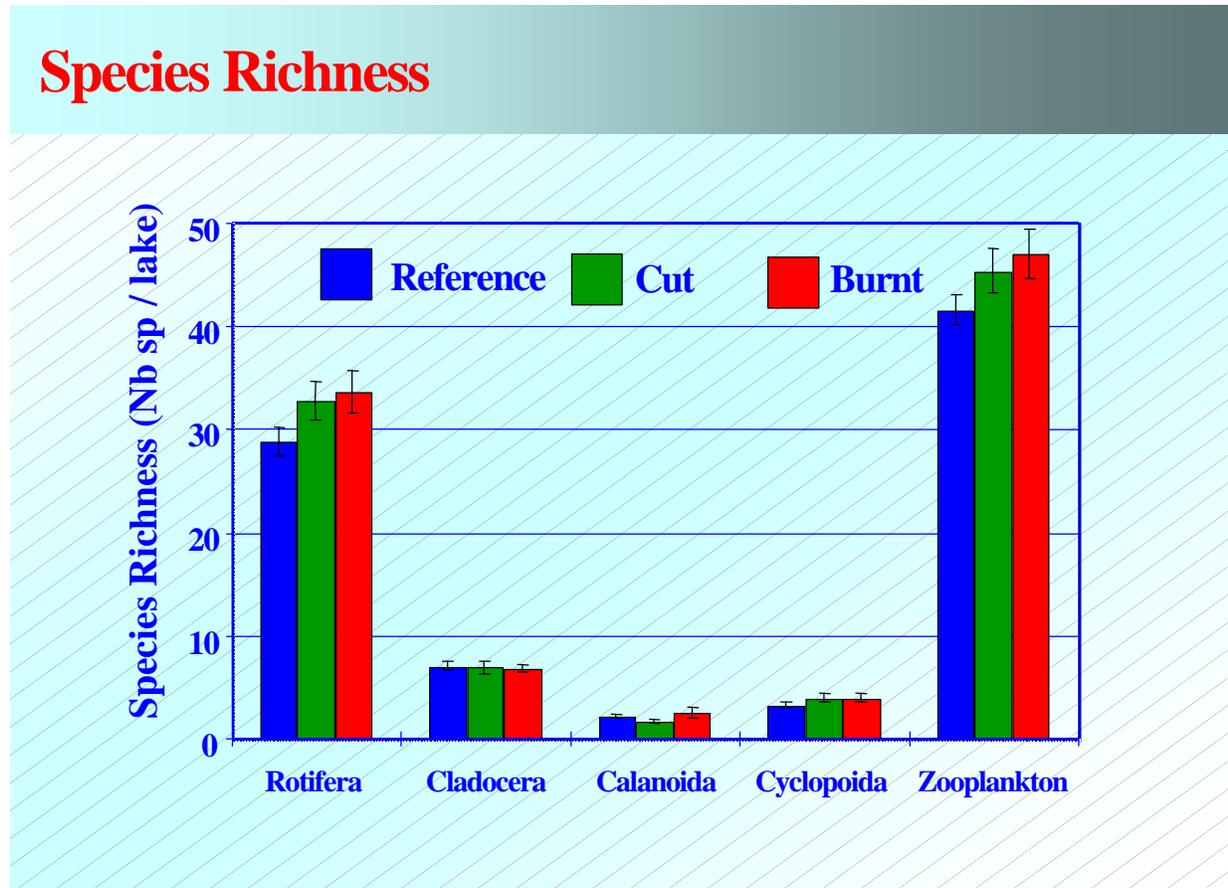
Diaphanosoma leuchtenbergianum and *Holopedium gibberum*, while *Leptodiptomus minutus* and *Epischura lacustris* were the most frequent calanoid copepods, and *Cyclops scutifer*, *Mesocyclos edax* and *Diacyclops bicuspidatus thomasi* the most frequent cyclopoid copepods.

Figure 2: Total number of zooplankton species in Boreal Shield lakes and distribution among the three groups of lakes (reference, cut, burnt).



Total species richness per lake varied from 33 to 64, with a median value of 49 species. Mean species number varied from 29.2 ± 1.2 in the reference lakes to 31.2 ± 2.4 in the cut lakes, and 34.6 ± 1.5 in the burnt lakes (Fig. 3). Rotifers made most of the species richness with between 18 to 45 species per lake (median of 31). Total cumulative diversity, based on Shannon Index, varied between 1.97 to 2.94, with a median of 2.5 (data not shown).

Figure 3. Species Richness (mean and standard deviation for total zooplankton and each taxonomic groups (Rotifera, Cladocera, Calanoida, and Cyclopoida) in the three groups of lakes (reference, cut, burnt) in 1996. From Patoine et al (2000b)

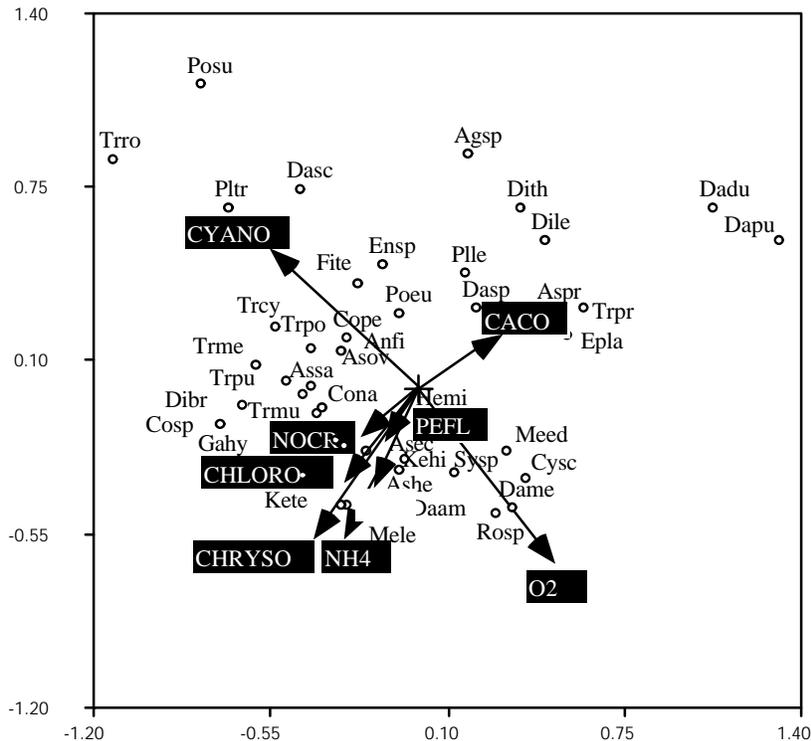
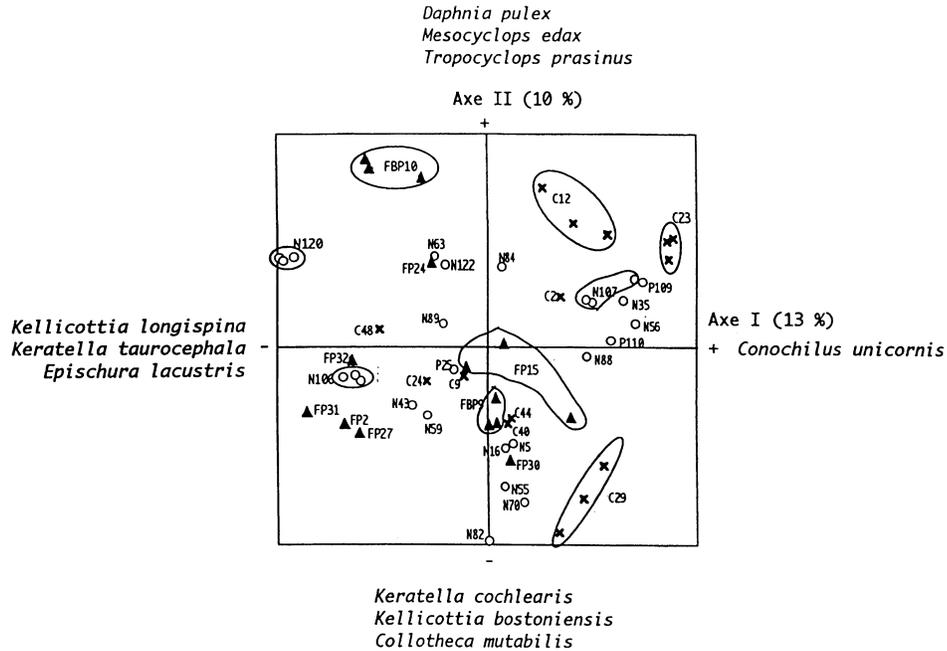


Natural fires or logging have minor impact on zooplankton biodiversity and species assemblages in boreal lakes, at least at short term. One year after watershed disturbances, no significant differences were found in zooplankton species richness or Shannon diversity index among the three groups of lakes for total zooplankton and all taxonomic groups ($F_{2,35} \leq 2.27$; $P > 0.12$). Nonetheless, total cumulative species richness tended to be higher in both cut and burnt lakes by 9% and 11% respectively (Fig. 3). The 4-5 extra species found per lake in cut or burnt lakes were also commonly found in reference lakes. The small increase in species richness in perturbed lakes reflected small increases in the number of species of rotifers and cyclopoids (+ 17%). No significant relationships between zooplankton species richness and environmental factors were found

Species assemblages in the 38 lakes are typical of the zooplankton community structure in Canadian Shield Lakes in Québec and Ontario (Pinel-Alloul et al. 1990; Keller and Conlon 1994). Species assemblages does not differ among the three different watershed conditions, as shown by PCA and CCA analyses (Fig. 4). There is no cluster of species specific to each of the three watershed conditions. Within-lake variation in species assemblages (between replicates) is very small compared to among-lakes. Shifts in species among different watershed conditions concerned species of minor importance representing less than 1% of total zooplankton abundance (Patoine et al. 2000b). Only 3% of the total variance in zooplankton species assemblages is explained by watershed condition ($P = 0.05$), with significant difference among burnt and reference lakes only ($P = 0.03$). When watershed condition was expressed as a continuous variable (% of watershed area disturbed either by fire or logging), the amount of total variance explained decreased to 1.5%, but was still significant. However, summer sampling periods (months) accounted for a higher percentage of total variance in zooplankton species assemblages (9.5%) than the watershed conditions.

The forward selection procedure selected 13 environmental factors which explained 23.4% of the total variance in species assemblages. The major environmental gradients related to variation in species assemblages are i) the Oxygen/Cyanobacteria gradient which reflects seasonal patterns (higher oxygen in June and higher cyanobacteria biomass in September), and ii) the White sucker/Chrysophytes biomass gradient which is related to changes in fish community among lakes and low biomass of Chrysophytes in July. There was no apparent tendency for zooplankton species to cluster according to watershed conditions when CCA analysis is constrained by these environmental factors, suggesting again that lakes belonging to different watershed conditions share similar zooplankton communities. The amount of variance that could be explained by watershed conditions alone, independently of the 13 environmental variables amounted to 1.7% and was not significant ($P = 0.20$), while the 22.4% of variance associated with the 13 environmental factors, independently of watershed conditions, remained significant ($P = 0.01$) (Patoine et al. 2000b).

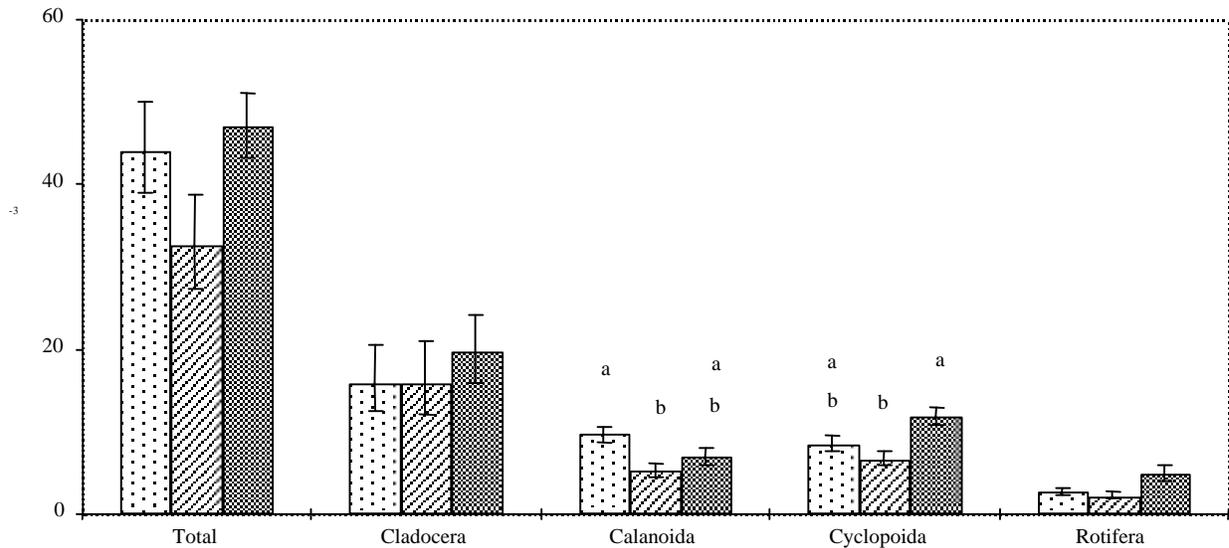
Figure 4. Clustering of lakes (n =38) and sampling replicates in 9 lakes (in circles), in the first PCA ordination plan based on the similarity of species assemblages in lakes in each group (reference, logged, burned) in July 1996. N or P refer to the reference lakes, C to the logged lakes, and F to the burned lakes. Discriminant species correlated with the PCA axes are listed on each side of the ordination plan. From Pinel-Alloul et al. (1998) and Patoine et al. (2000b)



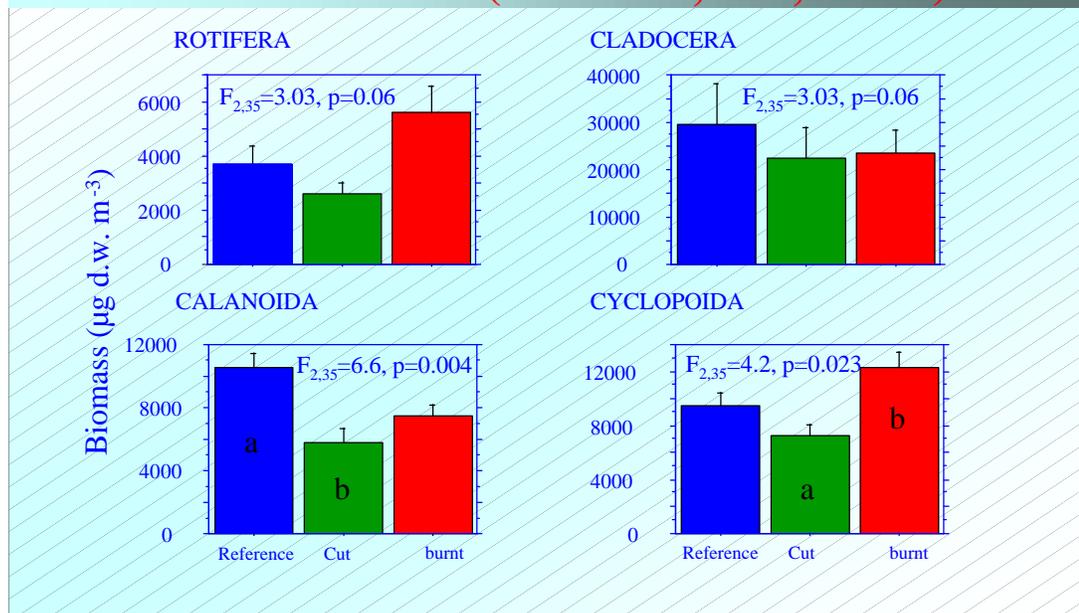
Zooplankton Biomass

Total zooplankton biomass varied between 19 and 170 mg d.w.m⁻³; the mean biomass was 48 mg d.w.m⁻³ for the 38 lakes. They were comparable to zooplankton biomass in boreal lakes in Ontario of comparable trophic status (TP: 5 to 18 µg/l) and lake area (10 to 124 ha) (Yan 1986). Our hypothesis of higher zooplankton biomass in cut and burnt lakes was not fully supported. Natural fires and logging have different impacts on zooplankton biomass in boreal lakes. Similarly to our initial hypothesis, we found a trend for higher total zooplankton biomass in burnt lakes than in reference lakes, but the cut lakes showed the inverse pattern (Fig. 5). Overall, the biomass of total zooplankton showed no statistically significant variations among the three groups of lakes ($P > 0.25$), although burnt lakes consistently showed higher biomass values than the reference lakes (Fig. 5). Among-group significant differences in zooplankton biomass occurred mainly for the copepods, whereas cladocerans and rotifers showed no or weak changes (Fig. 5). Calanoid biomass was 43 % lower in cut lakes than in reference lakes ($P = 0.04$), while cyclopoid biomass was 43 % lower in cut lakes than in burnt lakes ($P = 0.023$). Among-group variation in rotifer and cladoceran biomass was marginally significant ($P = 0.06$). Rotifers showed a pattern similar to that of cyclopoids whereby cut lakes supported 54% less rotifer biomass than burnt lakes. Cladocera biomass tend to be lower in perturbed lakes relative to reference lakes.

Figure 5. Among-group differences in the 1996 mean biomass of total zooplankton and taxonomic groups (mg d.w.·m⁻³). From left to right, bars represent undisturbed- (light stippling), cut (hatched) and burnt lakes (shaded). Error bars represent one standard error. Bars with different letters represent groups with significantly different means ($\alpha = 0.05$, Duncan multiple range test).



Taxonomic groups biomass in 1996: effects of watershed conditions (reference, cut, burnt)



Given the natural variability of zooplankton biomass in the reference lakes (Table 2), our study design could not have allowed us to declare as significant any mean difference smaller than 30% for the biomass of total zooplankton and copepods (calanoids and cyclopoids). The cladocerans and rotifers are exceptions; they showed important variations among the reference lakes in that their upper 95% confidence limits extended to 69% and 45% respectively of the mean. Considering the low number of cut and burnt lakes (9) compared to the reference lakes (20), it was therefore difficult to detect significant changes in the biomass of these zooplankton groups among the three watershed conditions.

Table 2. Mean biomass variability in reference lakes in 1996 (n=20). Mean and 95% confidence limits around the mean were back-calculated from log-transformed data on which ANOVAs were performed. The relative differences between confidence limits and means are indicated in parentheses.

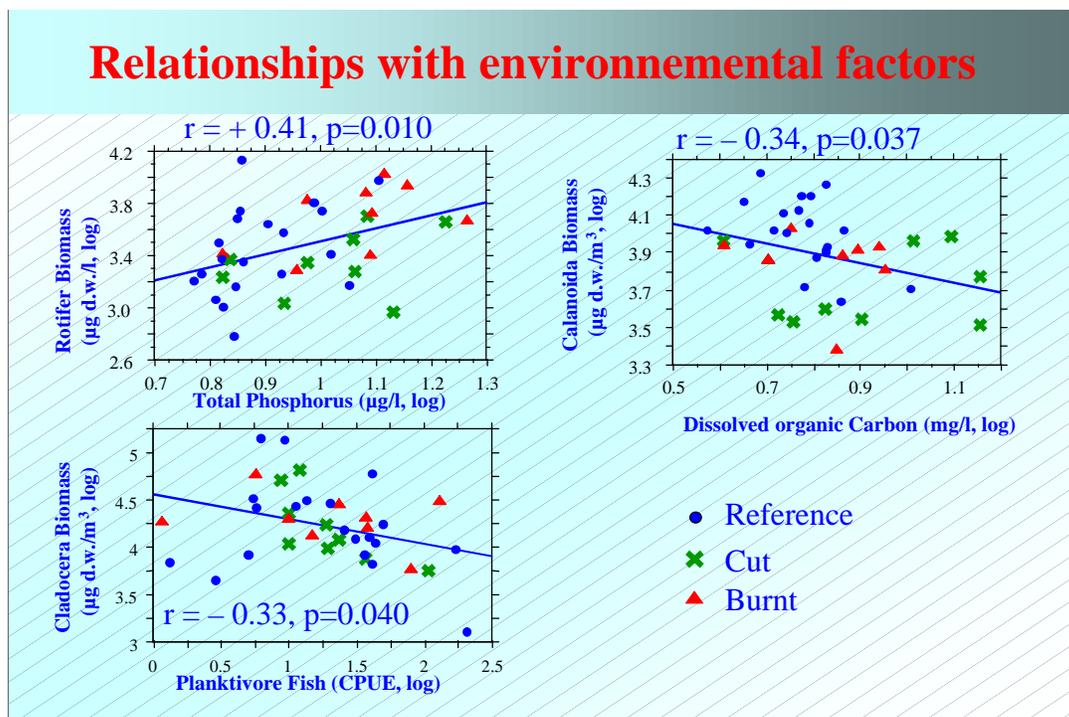
Variables	Mean	Lower 95% confidence limit	Upper 95% confidence limit
Total zooplankton (mg d.w.·m ⁻³)	44.1	34.0 (23%)	57.3 (30%)
Cladocerans (mg d.w.·m ⁻³)	16.0	9.4 (41%)	27.0 (69%)
Calanoids (mg d.w.·m ⁻³)	9.7	7.9 (18%)	11.8 (22%)
Cyclopoids (mg d.w.·m ⁻³)	8.5	6.8 (20%)	10.6 (25%)
Rotifers (mg d.w.·m ⁻³)	2.7	1.9 (31%)	3.9 (45%)
Total limnoplankton (mg AFDW·m ⁻³)	52.8	45.4 (14%)	61.5 (16%)
Crustacean size fraction (mg AFDW·m ⁻³)	12.7	9.5 (25%)	16.9 (33%)
Copepodite size fraction (mg AFDW·m ⁻³)	18.1	15.2 (16%)	21.5 (19%)
Rotifer size fraction (mg AFDW·m ⁻³)	10.5	8.8 (16%)	12.4 (19%)
Algae size fraction (mg AFDW·m ⁻³)	9.6	8.3 (13%)	11.0 (15%)

Contrary to our expectations, there was a general tendency for cut lakes to support biomass of zooplankton equivalent or lower (calanoids) to those of reference lakes (Fig. 5), despite higher TP concentrations (Table 1). When examining the absence of difference in zooplankton biomass between reference and cut lakes, one must consider the difference in the

intensity of disturbance between the logged and burned groups of lakes. Forestry practices removed on average 44% of forest cover in the logged group while natural forest fires removed on average twice that proportion in burned lakes (Table 1). In addition, Québec provincial legislation requires that a 20 m buffer strip zone of unharvested vegetation be left along lakes and streams. The lower degree of disturbance and the buffer strips might have mitigated the nutrient inputs to cut lakes, thus in part accounting for the absence of detectable zooplankton biomass differences between cut and reference lakes.

Contrary to other zooplankton groups, calanoid biomass was lower in cut lakes than in reference lakes. 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 DOC ($r = -0.34$, $P = 0.037$), TN ($r = -0.4$, $P = 0.01$) and Chl-*a* ($r = -0.33$, $P = 0.05$). This suggests that calanoids did better in the clear and nutrient-poor environments of reference lakes than in the richer and coloured cut lakes. Rotifer biomass was positively related to TP concentrations in lakes and responded to nutrient inputs in perturbed lakes ($r = 0.41$, $P = 0.01$). Finally, Cladocera biomass was not related to nutrients input or watershed conditions but declined with the abundance of planktivorous fish ($r = -0.33$, $P = 0.04$).

Figure 6. Relationships between biomass of taxonomic groups and environmental factors.



Limnoplankton Biomass

Mean biomass of total limnoplankton varied between 19 and 154 mg AFDW.m⁻³, and averaged 65 mg AFDW.m⁻³ for all 38 lakes over the three year survey (1996-98). Natural fires increase limnoplankton biomass in burnt lakes, whereas logging never affects the biomass of limnoplankton in cut lakes relative to reference lakes (Fig. 6). Burnt lakes tended to support 57% more of total limnoplankton biomass than reference lakes, 64% more of the crustacean size fraction and 53% more of the rotifer size fraction. The rotifer size fraction was also 55% more abundant in burnt lakes than in reference and cut lakes during the first year after disturbance. The highest increases in the biomass of total limnoplankton and size fractions occurred two years after disturbances. This increase in limnoplankton biomass in burnt lakes relative to reference lakes are consistent with the greater TP, TN and Chl-*a* concentrations observed in the burnt lakes (Table 1) and the positive relationships reported between zooplankton biomass and TP and TN (Yan 1986), or Chl-*a* (Pace 1986) in North-American lakes. In contrast, our results suggest that cut lakes tended to support similar or lower zooplankton biomass than the reference lakes despite higher TP and TN concentrations due to higher DOC and colour in waters which induced light limitation of algal production.

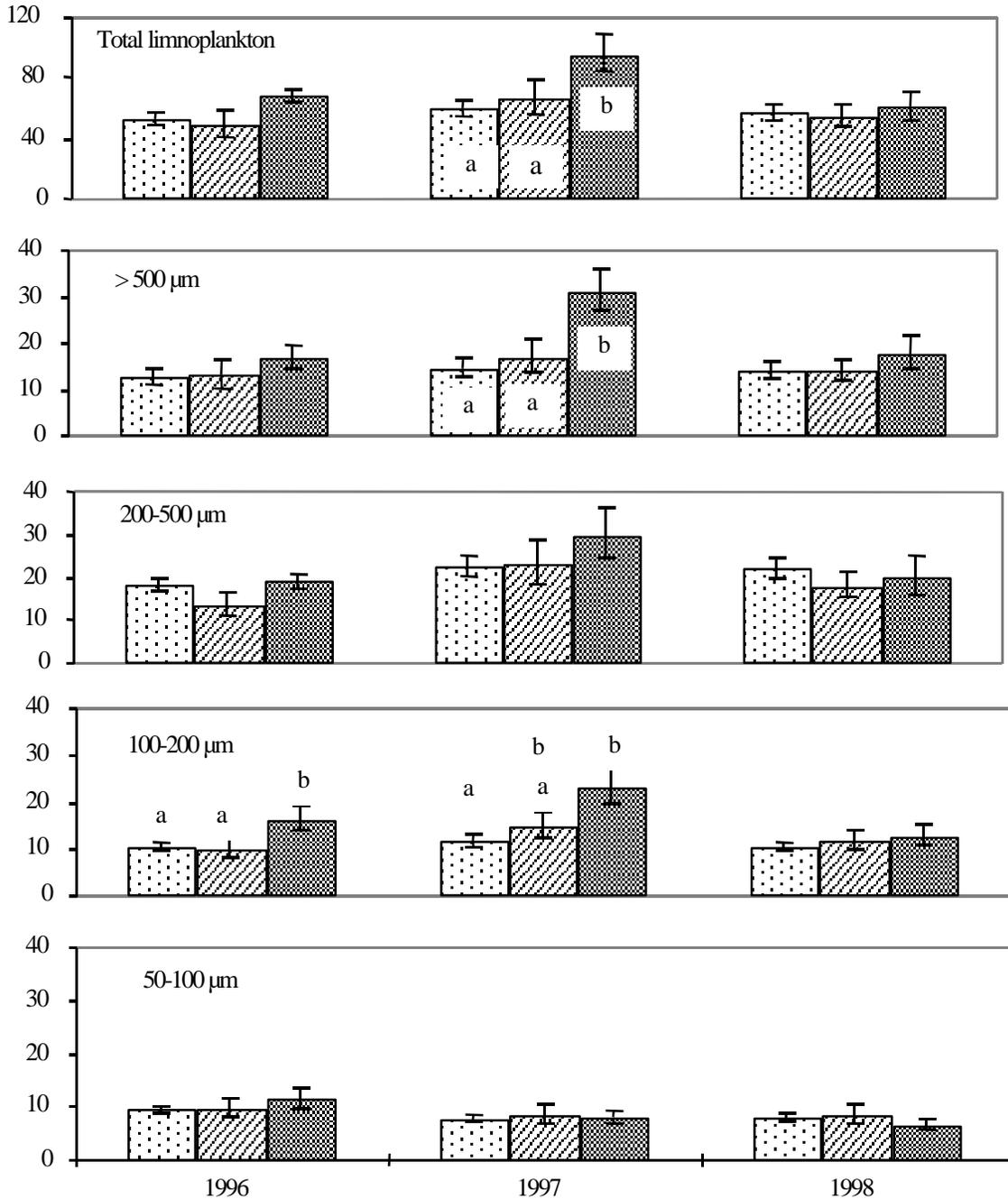
It is interesting to note that burnt lakes supported greater biomass of the crustacean size fraction than reference lakes during the second year, but not during the first year following fire disturbance, unlike the rotifer size fraction. This could reflect the shorter generation time of rotifers relative to crustaceans (Allan and Goulden 1980), allowing rotifers to exploit the increase in available food resources following fires before the crustaceans. Rotifers, and more generally small-size zooplankton, known as r strategists, are related more closely to increases in nutrients and algal resources in Eastern Canadian oligo-mesotrophic lakes (Currie et al. 1999). In contrast, crustaceans, and especially copepods known as K strategists, tend to express time lags in response to increases in nutrient concentrations (Smith 1969). Alternatively, the greater biomass of the crustacean size fraction in burnt lakes relative to reference lakes observed during the second year could be the result of a lower planktivory pressure in the burnt lakes (Brooks and Dodson 1965). Although coarse data on planktivorous fish CPUE provide no indication of differences in planktivory pressure among the three groups of lakes (Table 1), St-Onge and Magnan (2000) reported lower abundance of juveniles of yellow perch after fires, which might have reduce fish predation on large crustaceans.

Given the natural variability in limnoplankton biomass in the reference lakes (Table 2), our study design could not have allowed us to declare as significant any mean difference smaller than 33%. However, limnoplankton biomass variables appeared to be more conservative than

zooplankton biomass attributes, showing lower natural variation. Therefore, limnoplankton biomass has a good potential as indicator of changes in zooplankton communities in boreal lakes following watershed disturbances by fire or logging.

The year 1998 was characterised by an absence of among-group variations in limnoplankton biomass, since the three groups of lakes supported similar biomass levels in all size fractions and total limnoplankton (Fig. 6). This might indicate that the trophic enrichment produced by natural fires does not last more than 2 years, and the impacts of watershed disturbances are on short term. In other hand, the lack of effect in 1998 might be explain by climatic variation. Runoff was low in 1998 (dry year) in comparison to 1997 (wet year) (Lamontagne et al. 2000) and consequently export of nutrients might have been lower in 1998. Nevertheless, we could not conclude that the bottom-up cascading effect of higher nutrient inputs on the limnoplankton biomass, as observed in 1996 and mostly in 1997, tended to fade away during the third year because TP and Chl-a continued to be higher in burnt and cut lakes in 1998 (Carignan et al. 2000; Planas et al. 2000).

Figure. 6. Among-group differences in total limnoplankton and the four size fractions during the years 1996, 1997 and 1998 (mg AFDW•m⁻³). From left to right, bars represent undisturbed- (light stippling), cut (hatched) and burnt lakes (shaded). Error bars represent one standard error. Bars with different letters represent groups with significantly different means ($\alpha = 0.05$, Duncan multiple range test).



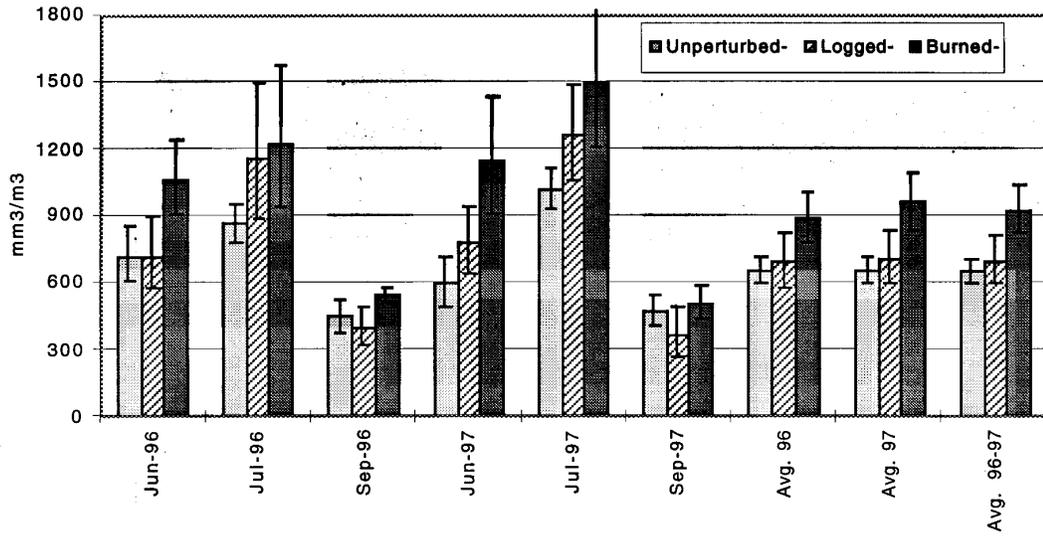
Crustacean biovolume, mean size and size spectra

Crustacean biovolumes and size were highly variables in the 38 lakes surveyed in 1996 and 1997. In general higher crustacean biovolumes and mean sizes were observed in perturbed lakes than in reference lakes at each sampling date and in 1996 and 1997 (Fig. 7). Means of crustacean biovolume were 655, 700 and 923 mm^3/m^3 , respectively for reference, cut and burnt lakes. Total crustacean biovolume was significantly higher in burnt lakes than in reference lakes, while it did not differ between cut and reference lakes ($F = 5.4$; $P = 0.05$). Mean size of crustaceans were 619, 701 and 753 μm , respectively in reference, cut and burnt lakes. It was higher in cut (13%) and burnt (22%) lakes than in reference lakes ($F = 10.5$; $P = 0.0001$).

PCA ordination served to describe spatial variation in crustacean size spectra among lakes. Some examples of crustacean size spectra in reference (P110f, N63b), cut (C9f, C40e) and burnt (FP32d, FP30d, FBP9d, FBP10d) lakes are presented in Figure 8. The first two axis of the PCA ordination accounted for a total of 74% of the total variance in the size spectra (Fig. 9). Axis I (58% of total variance) was positively correlated with biovolumes of all size classes, but most strongly with large size classes (1200-1300 μm , 1300-1400 μm and 1400-1500 μm). Samples from burnt lakes generally ranked higher along PCA axis I than samples from references lakes (Fig. 8), suggesting that crustacean biovolume in the 1200-1500 μm size classes were significantly higher in burnt lakes than in the reference lakes. Axis II (16% of the total variance) represented variation in biovolumes of 900-1100 μm (positive loading) and 1600-1800 μm (negative loading) size classes.

Watershed condition (reference, cut, burnt) was a significant source of variation in PCA scores along axis I (Table 3), indicating that burnt lakes had significant higher scores on axis I than reference lakes,; cut lakes had intermediate scores not significantly different from those of the reference or burnt lakes. Water shed condition was not a significant sources of variation in PCA scores on axis II (Table 3A). However, the nested ANOVA indicated that the month of sampling was a more important source of variation in size spectra than watershed condition (Table 3B).

Figure 7. Crustacean biovolume and mean size (mean \pm standard error for each group of lakes (unperturbed, logged and burnt) at each sampling month and in average in 1996 and 1997 and overall in 1996-97.



B)

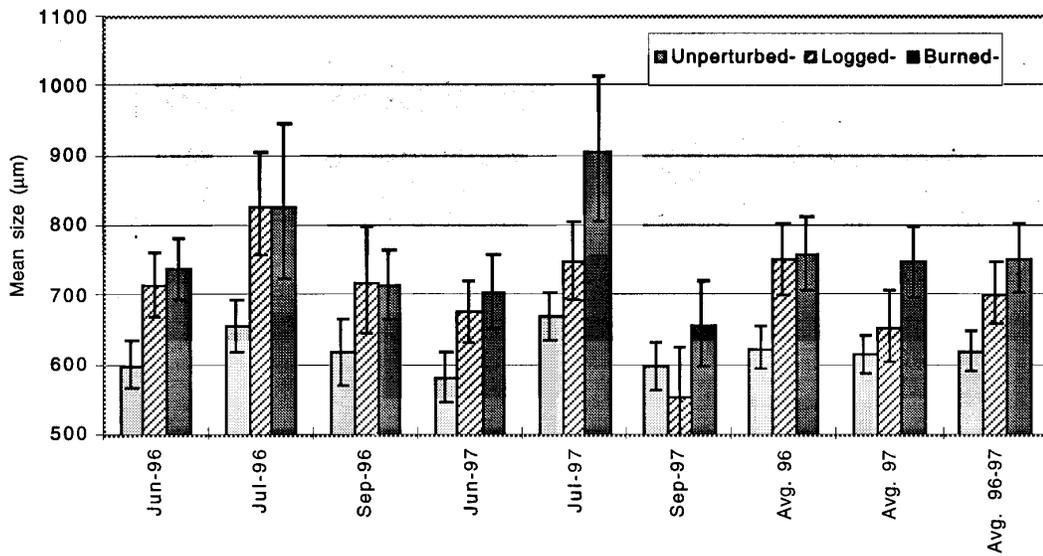


Figure 8. Examples of size spectra that illustrate how biovolume in each size class changes as one progress from low axis I PCA scores (left-most column) to high ones (right-most column), and from low axis II PCA scores (bottom row) to high ones (upper row). The horizontal axis represents 22 size classes, 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/m^3 units.

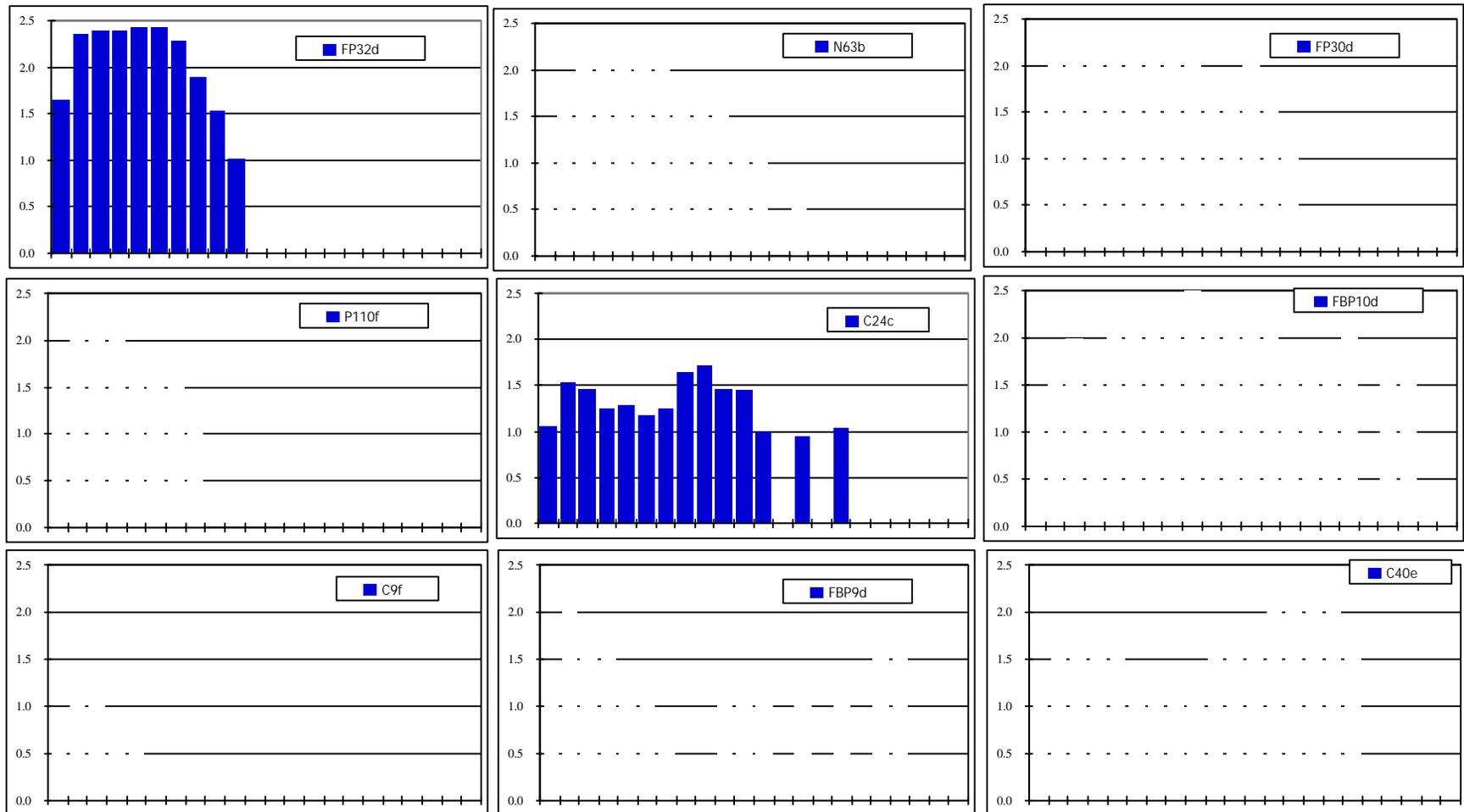


Table 3. Results of analysis of variance performed on PCA axis I scores (Book 17, p. 74, based on PCA with 19 descriptors ***replace with PCA based on 22 descriptors***).

A) Three level mixed-model with month nested in year, year nested in lakes.

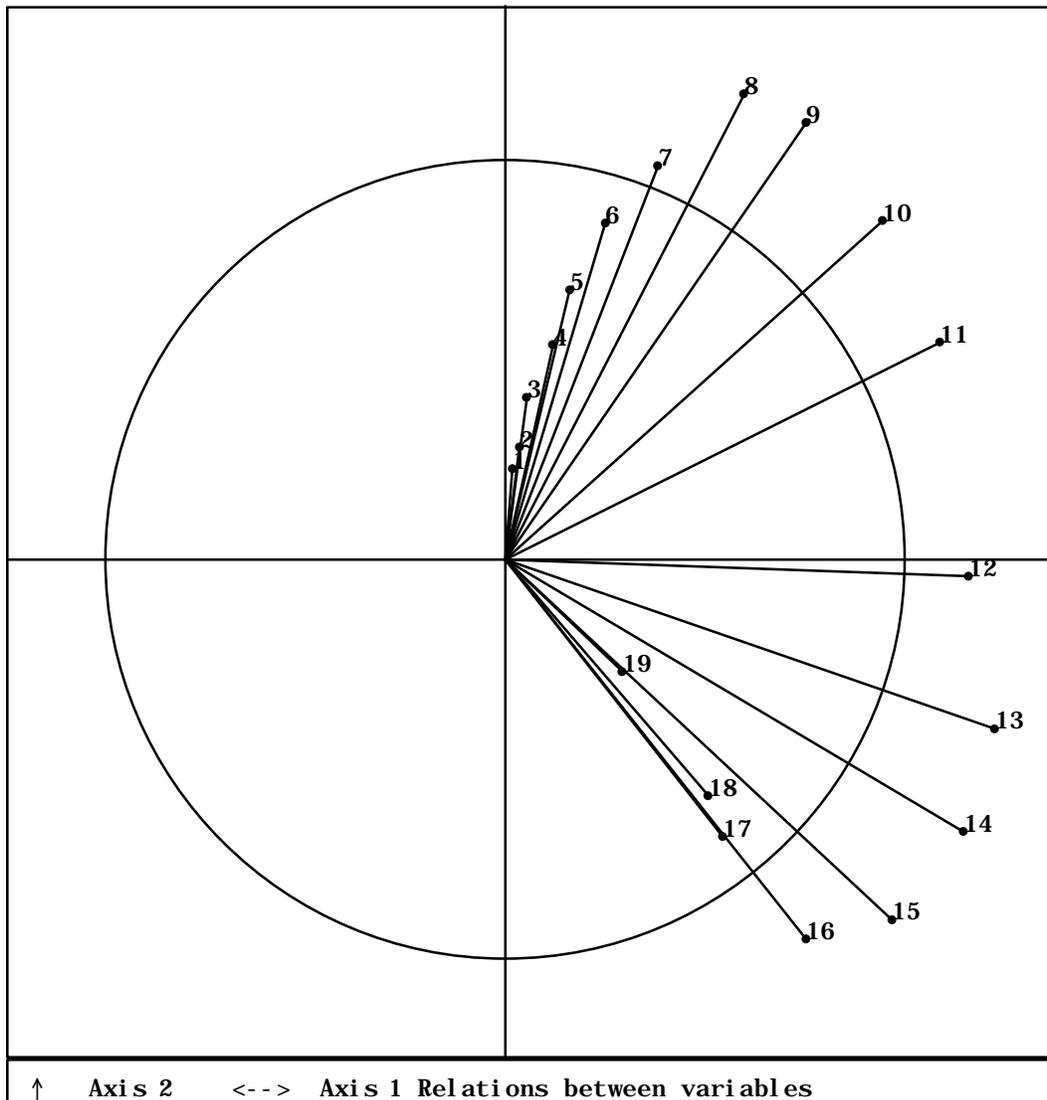
Source	DF Num	SS	MS Num	F Ratio	Prob>F	Variance component	% variance under mixed model	% variance assuming pure model II
Watershed condition	3 (4-1)	75.1	25.0	3.05	0.0415	0.355		10%
Lakes	34 (38-4)	278.5	8.2			0.936	28%	25%
Year	38 (76-38)	65.6	1.7			-0.327	-10%	-9%
Month	152 (228-76)	411.3	2.7			2.706	82%	74%

B) Two level mixed-model with sampling period nested in lakes.

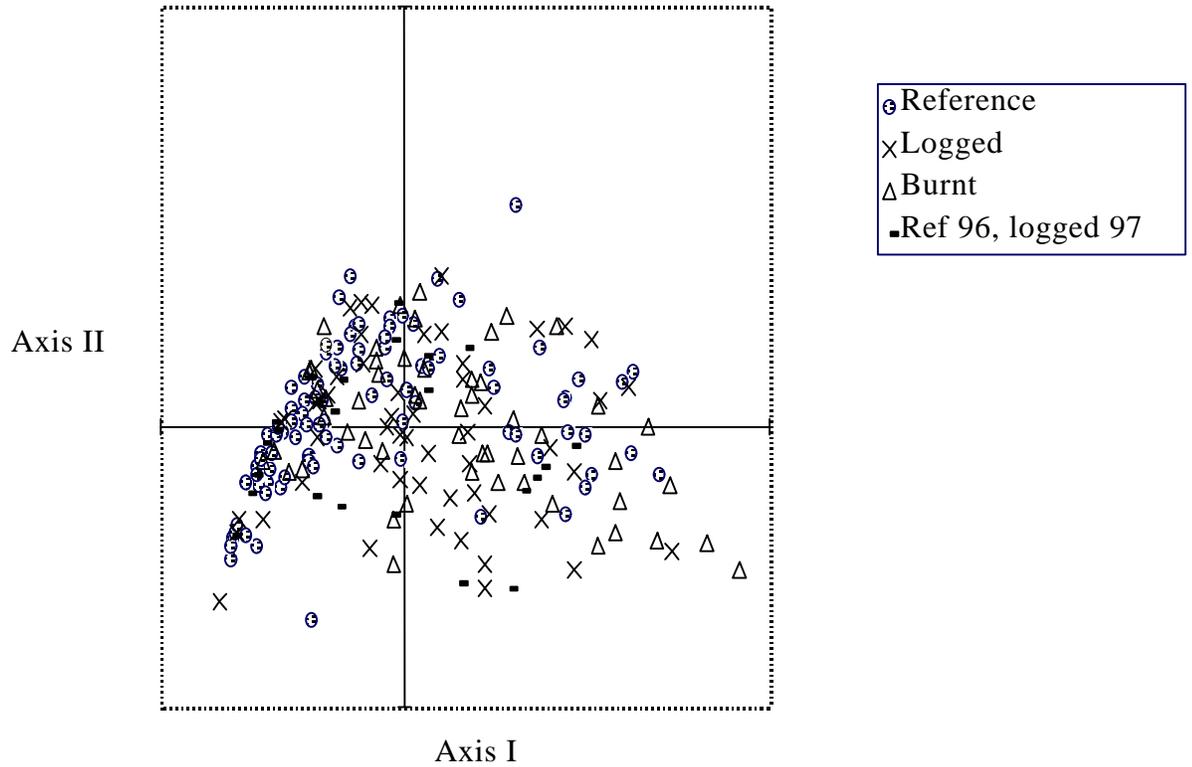
Source	DF Num	SS	MS Num	F Ratio	Prob>F	Variance component	% variance under mixed model	% variance assuming pure model II
Watershed condition	3	75.1	25.0	3.05	0.0415	0.317		8%
Lakes	34	278.5	8.2	3.26	<0.0001	0.947	27%	25%
Residual (sampling period)	190	477	2.5			2.510	73%	67%

Figure 9. 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 300-400 μm size class and so on). An angle near 0° between a size class vector and a principal component axis indicates a strong positive correlation of size class biovolume with the axis, whereas an angle near 180° indicates strong negative correlation. B) Plot of the 228 samples coded according to watershed condition.

A)



B)



Sources of Variation

We assessed the relative importance of watershed conditions, and sampling periods (months) as sources of variation in zooplankton attributes based on taxonomy, limnoplankton and size spectra data (Table 4). We found that sampling periods accounted for higher percentages of variation (8.3 to 37.8%) than watershed conditions (1.2 to 8.3%) for all zooplankton and limnoplankton attributes, except for the calanoid group and the copepodite size fraction for which both sources of variation were equivalent. The residual variation due to lake-to-lake changes in limnological conditions was the most important source of variation, accounting from 61 to 95% of the total variation (Patoine et al. 2000a). The greatly higher variation observed among lakes than among watershed conditions in zooplankton and limnoplankton biomass makes difficult to discern significant impact of watershed disturbances on the zooplankton community. It also emphasises the need to do long-term survey at the regional scale in attempt to evaluate the amplitude of the natural variability of aquatic communities. We should also take in account changes in watershed physiography and lake

characteristics when predicting the effects of watershed disturbances on aquatic ecosystems in the boreal forest.

Table 4. Relative importance of watershed condition and sampling period as factors accounting for the total variation in zooplankton biomass during the first year following watershed disturbance. Percentages represent ratios of the sum of squares associated with watershed condition and sampling period over the total sum of squares (log-transformed values).

Zooplankton group	Watershed condition	Sampling period
Total zooplankton (mg d.w.·m ⁻³)	2.5%	16.0%
Cladocerans (mg d.w.·m ⁻³)	1.4%	3.7%
Calanoids (mg d.w.·m ⁻³)	9.5%	8.3%
Cyclopoids (mg d.w.·m ⁻³)	1.2%	15.6%
Rotifers (mg d.w.·m ⁻³)	5.1%	27.2%
Total limnoplankton (mg AFDW·m ⁻³)	5.3%	23.8%
Crustacean size fraction (mg AFDW·m ⁻³)	3.0%	14.0%
Copepodite size fraction (mg AFDW·m ⁻³)	5.5%	4.7%
Rotifer size fraction (mg AFDW·m ⁻³)	8.3%	24.5%
Algae size fraction (mg AFDW·m ⁻³)	1.6%	37.8%

Relationships with environmental variables

Pearson correlation coefficients between the biomass of the four different taxonomic groups of zooplankton and environmental variables were weak, reaching at most 0.41 (Table 5). Among the six variables in the water quality category, TP displayed the strongest correlation, but was a significant correlate only in the case of rotifers ($P = 0.01$). Chlorophyll *a* was a weaker correlate than TP, but was common to both the biomass of rotifers and calanoids ($P < 0.045$). K was a common correlate of rotifers, calanoids and cladocerans ($P < 0.038$). While rotifers and cladocerans showed positive correlations with water quality variables, calanoids consistently displayed negative correlations. Cyclopoids biomass showed no significant correlations with any of the six water quality variables. Top-down variables showed significant correlations with rotifer (positive with *Chaoborus* density) and cladoceran biomass (negative correlation with

planktivorous fish), but not with calanoid or cyclopoid biomass. The drainage ratio was negatively correlated with the biomass of calanoids.

Table 5. Pearson correlation coefficients between zooplankton biomass (total and taxonomic groups) and environmental variables for the 38 lakes in 1996. Correlations are based on log-transformed variables.

	Total zooplankton	Cladocera	Calanoida	Cyclopoida	Rotifera
Drainage Ratio	ns	ns	-0.37*	ns	ns
% Watershed Area Deforested	ns	ns	ns	ns	ns
pH	ns	ns	ns	ns	ns
TP ($\mu\text{g L}^{-1}$)	ns	ns	ns	ns	0.41*
TN ($\mu\text{g L}^{-1}$)	ns	ns	-0.40*	ns	ns
K ⁺ (mg L^{-1})	ns	0.34*	-0.34*	ns	0.36*
DOC (mg L^{-1})	ns	ns	-0.34*	ns	ns
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	ns	ns	-0.32*	ns	0.33*
Chaoborids (ind.m^{-3})	ns	ns	ns	ns	0.41*
Planktivores (CPUE)	ns	-0.33*	ns	ns	ns
Piscivores (CPUE)	0.45**	0.43**	ns	ns	ns

Note: ns , not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Limnoplankton biomass displayed higher correlation coefficients with environmental variables than did biomass of taxonomic groups, reaching up to 0.6 (Table 6). Among the water quality variables, TP, TN and Chl-*a* were significant correlates of total limnoplankton and the 100-200 μm and $> 500 \mu\text{m}$ size fractions during the first (also the 50-100 μm size fraction) and second years after deforestation. Among the predation variables, the density of *Chaoborus* larva showed significant correlations with the 50-100 μm , 100-200 μm and $> 500 \mu\text{m}$ size fractions; these were positive and restricted to the first year. Piscivorous density was positively correlated with the $> 500 \mu\text{m}$ size fraction in 1996. Among the morphometric variables, the proportion of watershed area deforested (by logging or fire) showed significant positive correlations with the biomass of all size fractions (except the 200-500 μm) and total limnoplankton during one year or the other (1996 or 1997). Drainage ratio was not a significant correlate for any of the size fraction, in any year. Unlike the first two years following watershed perturbation (1996 and 1997), there were few significant correlations in 1998; only the 100-200 μm size fraction showed positive correlations with TP, TN and Chl-*a*.

Table 6. Pearson correlation coefficients between limnoplankton biomass (size fractions and total limnoplankton) and environmental variables of the 38 lakes during 1996, 1997, and 1998. The year of the data on which the correlation is based is indicated in parenthesis. Correlations are based on logged variables. No data on fish catch per unit effort or *Chaoborus* larva density were available in 1998.

	Total	> 500 μm	200-500 μm	100-200 μm	50-100 μm
Drainage Ratio	ns	ns	ns	ns	ns
% Watershed Area Deforested	+0.37* ('96) +0.49** ('97)	+0.48** ('97)	ns	+0.44** ('96) +0.52*** ('97)	+0.34* ('96)
pH	ns	ns	ns	ns	ns
TP ($\mu\text{g}\cdot\text{L}^{-1}$)	+0.53*** ('96) +0.57*** ('97)	+0.45** ('96) +0.60*** ('97)	+0.36* ('97)	+0.55*** ('96) +0.51*** ('97) +0.38* ('98)	+0.57*** ('96)
TN ($\mu\text{g}\cdot\text{L}^{-1}$)	+0.34* ('96) +0.47** ('97)	+0.36* ('96) +0.44** ('97)	ns	+0.40* ('96) +0.41* ('97) +0.32* ('98)	+0.35* ('96)
K ⁺ ($\mu\text{g}\cdot\text{L}^{-1}$)	+0.34* ('96) +0.38* ('97)	+0.38* ('96) +0.48** ('97)	ns	+0.38* ('96) +0.37* ('97)	ns
DOC ($\text{mg}\cdot\text{L}^{-1}$)	ns	ns	ns	ns	ns
Chlorophyll <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	+0.38* ('96) +0.55*** ('97)	+0.47** ('97)	+0.34** ('97)	+0.48** ('96) +0.60*** ('97) +0.52*** ('98)	+0.50** ('96) +0.35* ('97)
Chaoborids (ind. $\cdot\text{m}^{-3}$)	ns	+0.34* ('96)	ns	+0.39* ('96)	+0.37* ('96)
Planktivores (CPUE)	ns	ns	ns	ns	ns
Piscivores (CPUE)	ns	+0.41* ('96)	ns	ns	ns

Note: ns, not significant ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Among the environmental factors, 2 variables (K and TP and white sucker CPUE) explained 18.6% of the total variance in crustacean size spectra (Patoine et al. 2000c). TP was shown to be directly proportional to the drainage ratio (catchment area/total lake area) and the relative importance of disturbances (logged or burnt catchment area/total lake area or volume. K and TP were considered as surrogate variables for the intensity of disturbances (Carignan et al. 2000). K and TP were positively associated to observed increases in large crustacean size classes (1200-1500 μm), suggesting a cascading bottom-up effect of disturbances on crustacean biovolumes. The negative relationship with white sucker CPUE suggest a top-down effect of watershed disturbances on zooplankton size structure through changes in the fish community. White sucker density are been showed to be positively related to planktivorous fish, and negatively related to piscivorous fish (Patoine et al. 2000c). Although the total density of fish species did not differ among the three groups of lakes, the proportion of small (< 120 mm) yellow perch was lower in perturbed lakes than in the reference lakes (St-Onge and Magnan, 2000). Since zooplankton represented on average 40% of the diet of small yellow perch (P. Magnan, pers. Com.), the increase in the biovolume of large crustaceans in burnt and logged lakes might be explained by decreased vertebrate predation in perturbed lakes relative to the reference lakes.

Table 7 displays the regression models that were developed for the zooplankton and limnoplankton variables, using the environmental variables that showed the highest significant correlation coefficients (Tables 5 and 6). No model was developed for cyclopoids because none of the environmental variables examined correlated significantly with cyclopoid biomass. In all cases, the coefficients of determination (r^2) did not exceed 58%. However the models suggest a significant bottom-up effect of nutrient inputs and increase in chlorophyll *a* over all 38 lakes, due mainly to the natural fire effect. In opposite, models indicate a negative effect of DOC due to the logging impact on water colour and the plankton development. However we did not found significant effect of watershed conditions (dummy variables: L or B) except in the case of the calanoids for which there is a significant negative effect of logging (L), and the case of the algal size fraction for which a negative correlation with natural fire was observed. In 1996, lakes having low planktivory pressure (high abundance of piscivores) are associated wit higher biomass of total zooplankton and cladocerans.

Table 7 . Regression models describing the best relationships between zooplankton and limnoplankton biomass and environmental variables.

Variable	Year	Model	R ²
Total zooplankton	'96	$Y = 4.49 + 0.27 (20\%) \log(\text{pisc})^{**}$	20%
Cladocera	'96	$Y = 4.00 + 0.47 (18\%) \log(\text{pisc})^{**}$	18%
Calanoida	'96	$Y = 5.46 - 0.63 (16\%) \log(\text{TN})^* - 0.21 (18\%) (L)^{**}$	34%
Cyclopoida	'96	None of the 11 environmental variables met the 0.05 significance level for entry into the model	
Rotifera	'96	$Y = 2.34 + 1.24 (17\%) \log(\text{TP})^{***} - 0.26 (11\%) (L \times \log \text{TP})^*$	28%
Total limnoplankt.	'96	$Y = 1.07 + 1.06 (27\%) \log(\text{TP})^{***} - 0.39 (19\%) \log(\text{DR})^{**} - 0.15 (12\%) (L \times \log \text{DR})^{**}$	58%
	'97	$Y = 1.34 + 1.18 (32\%) \log(\text{TP})^{***} - 0.73 (15\%) \log(\text{DOC})^{**}$	47%
	'98	None of the 11 environmental variables met the 0.05 significance level for entry into the model	
limno > 500 μm	'96	$Y = 0.37 + 0.81 (19\%) \log(\text{TP})^{**}$	19%
	'97	$Y = 0.50 + 1.56 (36\%) \log(\text{TP})^{***} - 0.83 (11\%) \log(\text{DOC})^*$	47%
	'98	None of the 11 environmental variables met the 0.05 significance level for entry into the model	
limno 200-500 μm	'96	None of the 11 environmental variables met the 0.05 significance level for entry into the model	
	'97	$Y = 1.12 + 1.02 (13\%) \log(\text{TP})^{**} - 0.83 (15\%) \log(\text{DOC})^*$	28%
	'98	None of the 11 environmental variables met the 0.05 significance level for entry into the model	
limno 100-200 μm	'96	$Y = 0.47 + 1.24 (29\%) \log(\text{TP})^{***} - 0.70 (16\%) \log(\text{DOC})^{**}$	45%
	'97	$Y = 0.66 + 1.11 (35\%) \log(\text{chl})^{***}$	35%
	'98	$Y = 0.71 + 0.85 (27\%) \log(\text{chl})^{***}$	27%
limno 50-100 μm	'96	$Y = -1.20 + 1.08 (33\%) \log(\text{TP})^{***} + 0.20 (17\%) \text{pH}^{***} - 0.67 (7\%) \log(\text{K})^*$	57%
	'97	$Y = 0.53 + 1.01 (12\%) \log(\text{chl})^* - 0.23 (15\%) (B)^*$	27%
	'98	None of the 11 environmental variables met the 0.05 significance level for entry into the model	

Note: *P<0.05, **P<0.01, ***P<0.001.

MANAGEMENT APPLICATIONS

Natural fires and logging each remove about 10,000 km² of Canada's 4.5 million km² forest each year (Forestry Canada 1991). New strategies in forest management are based on the assumption that emulating natural disturbances such as natural fires in logging practices will sustain boreal forest dynamics and biodiversity (Hunter Jr. 1993). Such strategies, however, were developed without considering aquatic ecosystems, even though water represents 8% of Canada's surface area. Comparing the impacts of natural fires and logging on lake water quality and biota is a necessary step towards forest management practices that take into account the global impacts of logging on the forest-lake ecosystem. Here, we outline the potential ecological consequences of watershed disturbances in boreal forest, either by natural fires or logging, based on the results of the research.

In one hand, potential ecological consequences of natural fire is a higher zooplankton biomass in burnt lakes two years after disturbance. This could mean more food for fish larvae and increased fish biomass in the following years. However, a five-fold increase in the daily ration may be necessary for a two-fold increase in growth rate of age I+ perch (Boisclair and Leggett 1989a). Although zooplankton biomass and fish food ration are two different things, the observed 64% increase in the mean biomass of the crustacean size fraction in burnt lakes relative to reference lakes is unlikely to represent a 500% increase in fish food ration. Moreover, zooplankton constitute a highly variable fraction of fish diet (Boisclair and Leggett 1989b).

In the other hand, potential ecological consequences of the observed 46% decrease in calanoid biomass (and cyclopoid to a lesser extent) in logged lakes relative to reference lakes may be of particular concern because these organisms likely constitute part of the diet of most fish larva and some adult fish in this region. If this food source is limiting for fish growth, and if fish cannot compensate by feeding on alternative food source (e.g. cladocerans), we can expect a low recruitment of fish in logged lakes in 1996. This was in fact supported by preliminary length frequency data for yellow perch and lake whitefish (St-Onge and Magnan 2000). If DOC can be shown to be responsible for this decrease in calanoid and cyclopoid biomass - as data herein suggest-, controlled burning of the slash left after logging could be a management option to mitigate DOC washout and associated decreased in calanoid biomass. However, as calanoids account for less than a quarter of total zooplankton biomass, the decrease in calanoid biomass observed in logged lakes is unlikely to lead to dramatic changes in fish growth rates.

The greater biomass of the rotifer size fraction in burnt lakes relative to reference lakes observed during the first and second year after disturbances could 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 most flow before reaching fish. The importance of such a phenomenon remains to be quantified.

The zooplankton biomass values reported in this study were similar to those reported in Yan (1986) for 16 unperturbed Ontario lakes with comparable lake area 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 the inter-annual, inter-month or inter-lake variability. Their data suggest these sources of variation were hard to untangle from that associated with watershed disturbance.

CONCLUSIONS

This study has shown that catchment deforestation can have impacts on lake ecosystems that are not limited to water chemistry, but extend to the zooplankton community as well. The nature, magnitude and timing of responses of the zooplankton community to watershed perturbation differ depending on the nature of the perturbation (logging or natural fires) and the taxonomic group or size class of zooplankton considered.

Even though specific groups or size fractions of the zooplankton communities showed biomass variations associated with both logging and forest fires, total biomass of zooplankton and limnoplankton varied significantly relative to reference lakes only in the case of burnt lakes. This variation in total zooplankton biomass was that of an increase in burnt lakes, that reaches the highest levels in the second year following watershed disturbance. However the variation in zooplankton biomass induced by fire disturbance is not greater than the summer month to month variations. Logging has a negative impact on the calanoids which are considered as indicators of clear and oligotrophic lakes. Our results suggest that zooplankton communities in Canadian Boreal Shield lakes experience small and transient increases following forest fires, but not following logging. The trophic enrichment in burnt lakes is linked to higher nutrient inputs from watershed and higher algal biomass. In contrast the lack of effect or the negative impact of

logging on calanoids is related to higher inputs of organic matter from watershed in logged lakes. Although watershed disturbances have significant impacts on zooplankton communities in boreal lakes, the main source of variation in zooplankton biomass remain the changes in watershed physiography and limnological characteristics among lakes, as well as zooplankton summer succession . The lack of trophic upsurge in logged lakes for the present case could also result of a lower intensity of disturbance than in burned lakes where natural fires removed on average twice the proportion of forest cover of watersheds as logging did. If the average proportion of watershed area logged by forestry companies were to increase, or if buffer zones were not to be left around lakes, a different picture might emerge.

Overall, empirical models relating zooplankton community with environmental factors in boreal lakes, showed a strong cascading effect of bottom-up factors (nutrient inputs and algal biomass) in burnt lakes. Negative impact of logging are related to increase in water colour and dissolved organic carbon in logged lakes. Even though watershed disturbances may significantly affect zooplankton community, the influence of watershed conditions is of low extent compared to the greater influence of season, watershed physiography and lake conditions. The extent of watershed disturbances either by fire or logging should be important (> 50% of the watershed area) to have important impact on lake plankton.

OPC analyses were used to determine and compare the impacts of natural fire and logging on crustacean size spectra. Overall, disturbances affect slightly crustacean size structure by increasing the biovolume and mean size of large crustaceans. This change might be explained both by bottom-up effects such as increase in runoff and nutrient inputs after fire and logging, or by top down effects due to lower recruitment in yellow perch and less predation pressure on large zooplankton .

A new study on experimental harvesting on Boreal Shield Lakes, underway since summer 2000, will allow us to validate the results and confirm trends and logging impacts noted during this comparative study.

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