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Bernadette Pinel-Alloul and Alain Patoine

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Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
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by

Bernadette Pinel-Alloul and Alain Patoine

Département de Sciences biologiques
Université de Montréal
C.P. 6128, Succ. Centre ville
Montréal (Québec)
Canada H3C 3J7

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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 the biomass, biodiversity and size structure of zooplankton communities in lakes of the Canadian Shield. The research was carried out from 1996 to 1998 in 38 lakes of the boreal forest in Québec; the watersheds of 20 of these lakes were not impacted, while 9 underwent logging and 9 underwent natural fires. Fire and logging occurred in 1995. Our study reveals that natural fire and logging disturbances have different impacts on zooplankton community of boreal lakes. Natural fires increase zooplankton biomass because of higher inputs of mineral nutrients (nitrates and phosphorus) from watersheds. Burned-watershed lakes supported on average 64% and 53% more biomass of cyclopoids and rotifers than reference lakes 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. Logged-watershed lakes supported on average 46% 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, logged- and burned-watershed lakes. The impacts of natural fire and logging on zooplankton biomass last only 2 years. Three years after watershed disturbances, the three groups of lakes supported equivalent biomass of all zooplankton taxonomic groups and size fractions. Neither natural fire and logging affect zooplankton biodiversity and species assemblages. Zooplankton biomass is a promising tools to monitor the effects of watershed disturbances by natural fire and logging on plankton production 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

Impacts of forest logging and natural fires were mostly assessed in lotic ecosystems. In streams, concentrations of particulate organic matter, phosphorus, nitrogen and ions increase after forest fires (Bayley et al. 1992) and clear-cutting (Likens et al. 1970). Following watershed disturbance, 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). In comparison to stream studies, little work has addressed the effects of the major watershed disturbances (natural fires and logging) on lake communities in the boreal forest. 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). The recent studies in Québec (SFM Network) suggest that deforestation, either through natural fires or logging, also tends to increase nutrient and organic carbon loading, as well as chlorophyll *a* and limnoplankton biomass in boreal lakes (Carignan et al. 1999). However, confounding factors such as the type of disturbance (logging or fire), the time elapsed since the disturbance, and the extent of natural variability in watershed physiography and limnological characteristics render any statement on the differential impacts of logging and fires on lake biota yet questionable.

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), 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 succeptible to affect bottom-up interactions and plankton (phyto- and zooplankton). It is therefore likely, but yet unknown, that zooplankton biomass in logged- and burned-watershed lakes should be somewhat higher than in unperturbed-watershed lakes. As fish yield and recruitement is strongly correlated to lake productivity and plankton food availability (Godbout and Peters 1988), any changes in zooplankton ressources may thereafter impact sportfish populations.

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 will be higher in logged- and burned-watershed lakes than in undisturbed-watershed lakes. We also assess the comparative effects of natural fire and logging on zooplankton biodiversity and species assemblages at short term (1 year after the perturbations). The relative influence of natural sources of variation (within- and among lake, season) and watershed conditions on zooplankton biomass was evaluated, as well as the relationships between zooplankton community attributes and the lake environmental characteristics (water chemistry, nutrients, organic matter, and planktivory pressure). More details on the preliminary results of the research are presented in Pinel-Alloul et al. (1998) and Patoine et al. 1999 (submitted).

STUDY SITE

The data were collected in 38 headwater lakes on the Boreal Canadian Shield. All the lakes are located within a 50,000 km^2 area around Réservoir Gouin, 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). The forest is primarily composed of black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), jack pine (*Pinus divaricata*), white birch (*Betula papyrifera*), and 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 60 years); 9 “logged” lakes, whose watersheds had undergone forest clearcutting over 8 to 96% fo their area, and 9 “burned” 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. The lakes were selected on the basis of comparable size, depth, watershed morphometries (Table 1), and time of the impact. All the lakes were stratified during summer and their watershed slope ranged from 7.5 to 19.5% (mean = 11.1%). 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). More details on bedrock geology, landscape features, climate and vegetation are presented in Garcia and Carignan (1999).

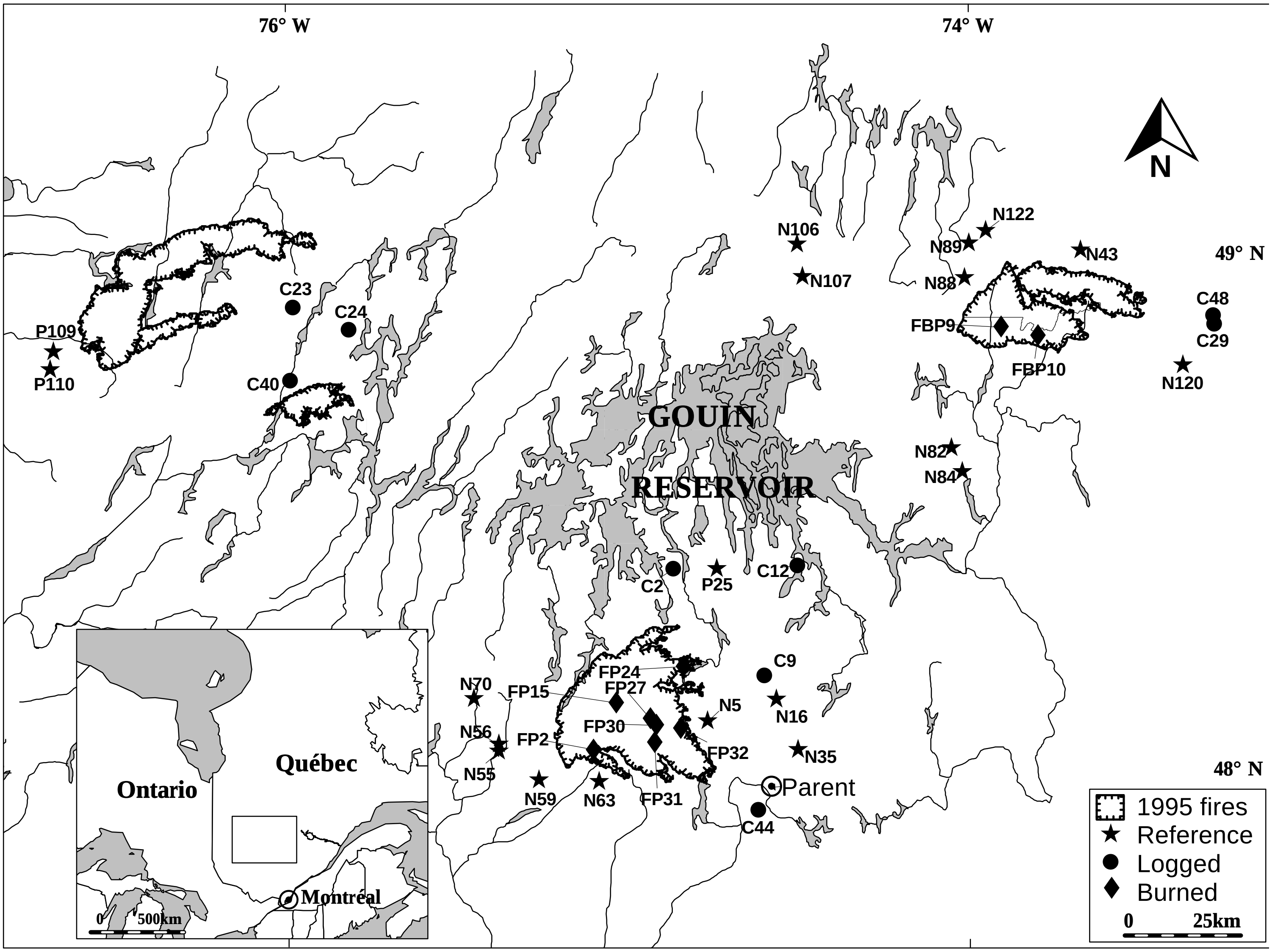

Figure 1. Location of study lakes. Letters N and P before lake numbers refer to reference lakes (stars), C refers to logged lakes (circles), and F to burned lakes (diamonds).

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)	Logged (n = 9)	Burned (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 ($\mu g \bullet L^{-1}$)	6.9 (4.5–11.8)	9.5 (5.4–17.3)	11.8 (5.6–17.3)
TN ($\mu g \bullet L^{-1}$)	213 (118–332)	252 (160–386)	310 (169–747)
K+ ($\mu g \bullet L^{-1}$)	232 (64–516)	521 (174–957)	754 (522–1152)
DOC ($mg \bullet L^{-1}$)	5.1 (2.5–9.1)	7.5 (2.7–13.2)	6.0 (3.0–9.3)
Chlorophyll *a* ($\mu g \bullet L^{-1}$)	1.7 (0.8–3.4)	2.0 (1.0–3.3)	3.1 (1.2–5.2)
Chaoborids ($ind. \bullet m^{-3}$)	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 field methods, laboratory procedures and statistical analyses can be found in Pinel-Alloul et al. (1998), Carignan et al. (1999), Garcia and Carignan (1999), and Patoine et al. (1999, submitted). Therefore, only a brief summary 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 6:00AM and 15:00PM. Water temperature and dissolved oxygen profiles were established at 0.5-m intervals with an electronic temperature/oxygen meter. Light attenuation and Sechhi depth were also measured. Nutrient (TP, TN, NO_3), dissolved organic carbon (DOC), chlorophyll *a* (Chl-a), and ions (K, Ca, Mg, Cl, SO_4) concentrations were estimated in the euphotic zone (see Carignan et al. 1999 for details on water chemistry 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.

Zooplankton Analysis[1]

In the laboratory, zooplankton samples were split into four equal fractions with a Folsom splitter; one quarter was used for taxonomic analysis, one was used for size fractionation and organic mass determination of limnoplankton. 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 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 four taxonomic groups (cladocerans, calanoids, cyclopoids and rotifers) and total zooplankton biomass. Zooplankton biomass was expressed in mg dry weight 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 fibber 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 weight measurements and expressed in mg of ash-free dry weight (AFDW) par 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 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, 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 algae size fractions respectively.

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[1] Taxonomic analysis of the zooplankton samples collected during the second (1997) and third (1998) years of the study is in progress. The long term changes in zooplankton community structure will be assessed later.

Statistical Analyses

We tested for statistically significant differences in biomass of zooplankton and limnoplankton among reference, logged- and burned-watershed lakes. 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). 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=5%), the Duncan multiple range test was performed to assess where differences lay (SAS Institute Inc. 1988). ANOVA was also performed on mean biomass values of limnoplankton and zooplankton variables to estimate the relative importance of different sources of variations (among replicates, among lakes, among sampling periods, and among watershed conditions).

To compare species assemblages and biodiversity of zooplankton in the three groups of lakes (reference, logged, burned), we used Steinhaus coefficients to perform clustering and Principal Coordinates analyses on the similarity matrix of species abundances of the 1996 July samples (Legendre and Legendre 1984).

Relationships between zooplankton and limnoplankton biomass and environmental variables were quantified by Pearson correlation (Sokal and Roff 1981). Environmental variables were grouped into three categories: water quality, predation and morphometry. The water quality category included pH, TP, TN, potassium (K), chlorophyll a (Chl-a) and dissolved organic carbon (DOC). The predation category included the density of *Chaoborus* larva (ind./m^3), the density of planktivorous fish and the density of piscivorous fish (St-Onge and Magnan 1999, submitted). Planktivorous fish included, in decreasing order of occurrence: yellow perch (*Perca flavescens*), fallfish (*Semotilus corporalis*), lake whitefish (*Coregonus clupeaformis*) and various cyprinids. Piscivorous fish included, in decreasing order of occurrence: northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*) and lake trout (*Salvelinus namaycush*). The morphometry category included drainage ratio (DR) and the proportion of the catchment area deforested by logging or forest fires (Table 1). Relationships between zooplankton and limnoplankton biomass attributes and the best environmental variables (highest Pearson correlations) were established.

All statistical analyses were performed on logged values. Logarithmic transformation was better than the square root transformation in rendering the variables equivariant among groups of lakes (ANOVA tests) and in linearizing the relationships (Pearson correlations, regression analyses).

SUMMARY OF RESULTS AND DISCUSSION

Zooplankton Biodiversity and Species Assemblages

Neither natural fires or logging have significant 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 among the three groups of lakes ($P = 0.09$). In July 1996, overall mean species number was 32 in the 38 lakes, including 19 rotifers, 5 cladocerans, 4 calanoids and 4 cyclopoids. Mean species number varied from 29.2 ± 1.2 in the reference lakes to 31.2 ± 2.4 in the logged lakes, and 34.6 ± 1.5 in the burned lakes (Fig. 2). The small increase in species number in the burned lakes is mainly due to an increase in the number of rotifer species (17.5 in the reference lakes vs 21.2 in the burned lakes). The most frequent species were *Keratella cochlearis*, *Kellicottia longispina*, *Conochilus unicornis*, *Polyarthra vulagaris*, *P. remata*, *P. major*, *Conochiloides dossuarius*, *Gastropus stylifer*, *Filinia terminalis*, *Keratella crassa*, *K. taurocephala*, *Kellicottia bostoniensis*, *Trichocerca elongata*, *Ploesoma lenticulare* and *Polyarthra euryptera* among the rotifers, *Bosmina* spp., *Daphnia longiremis*, *D. catawba*, *D. pulex*, *Diaphanosoma leuchtenbergianum* and *Holopedium gibberum* among the cladocerans, *Leptodiaptomus minutus* and *Epischura lacustris* among the calanoid copepods, and *Cyclops scutifer*, *Mesocyclos edax* and *Diacyclops bicuspidatus thomasi* among the cyclopoid copepods. These species assemblages 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 the clustering and PCoA analyses (Fig. 3). Within-lake variation in species assembalges is very small compared to among-lakes variations. There is no cluster specific to each of the three watershed conditions.

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 logged and burned-watershed 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 burned lakes than in reference lakes, but the logged lakes showed the inverse pattern (Fig. 4). Among-group significant differences in zooplankton biomass occurred mainly for the copepods, whereas cladocerans and rotifers showed no or weak changes (Fig. 4). Calanoid biomass was 46 % lower in logged-watershed lakes than in reference lakes while cyclopoid biomass was 43 % lower in logged- than in burned-watershed lakes. Among-group variation in rotifer biomass was marginally significant ($P = 0.06$) and showed a pattern similar to that of cyclopoids whereby logged-watershed lakes supported 54% less rotifer biomass than burned-watershed lakes. Despite a trend for higher biomass in the burned lakes than in the reference lakes, the biomass of total zooplankton and cladocerans showed no statistically significant variations among the three groups of lakes.

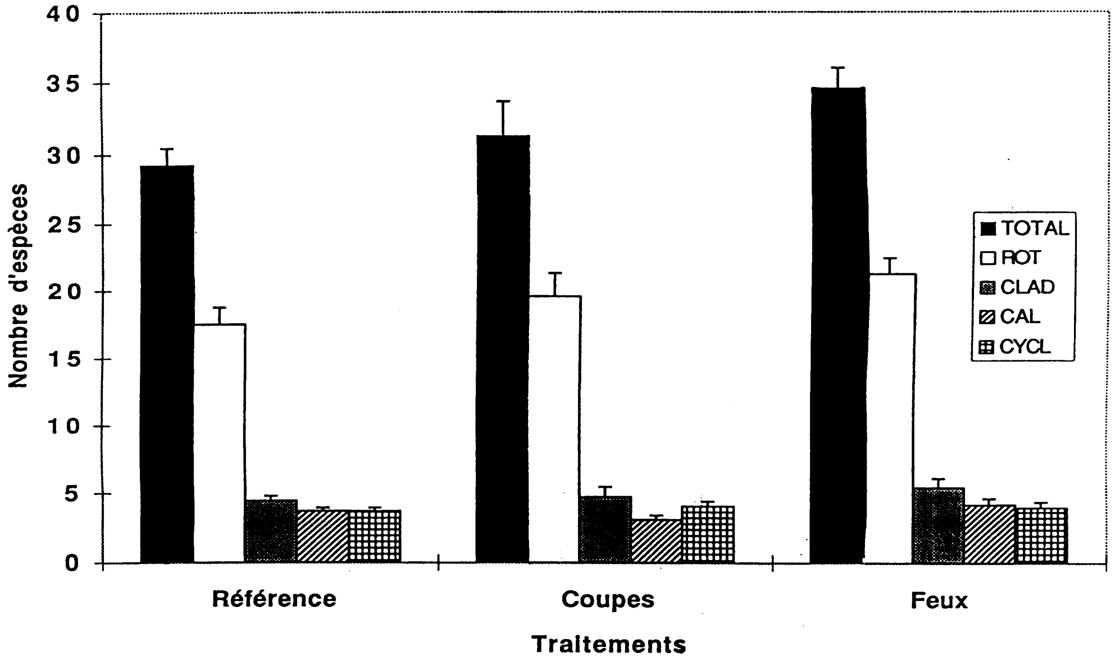


Figure 2. Species Richness (mean and standard deviation for zooplankton community (TOTAL), rotifers (ROT), cladocerans (CLAD), calanoid copepods (CAL), and cyclopoid copepods (CYCL) in the three groups of lakes (reference, logged, burned) in July 1996. From Pinel-Alloul et al. (1998).

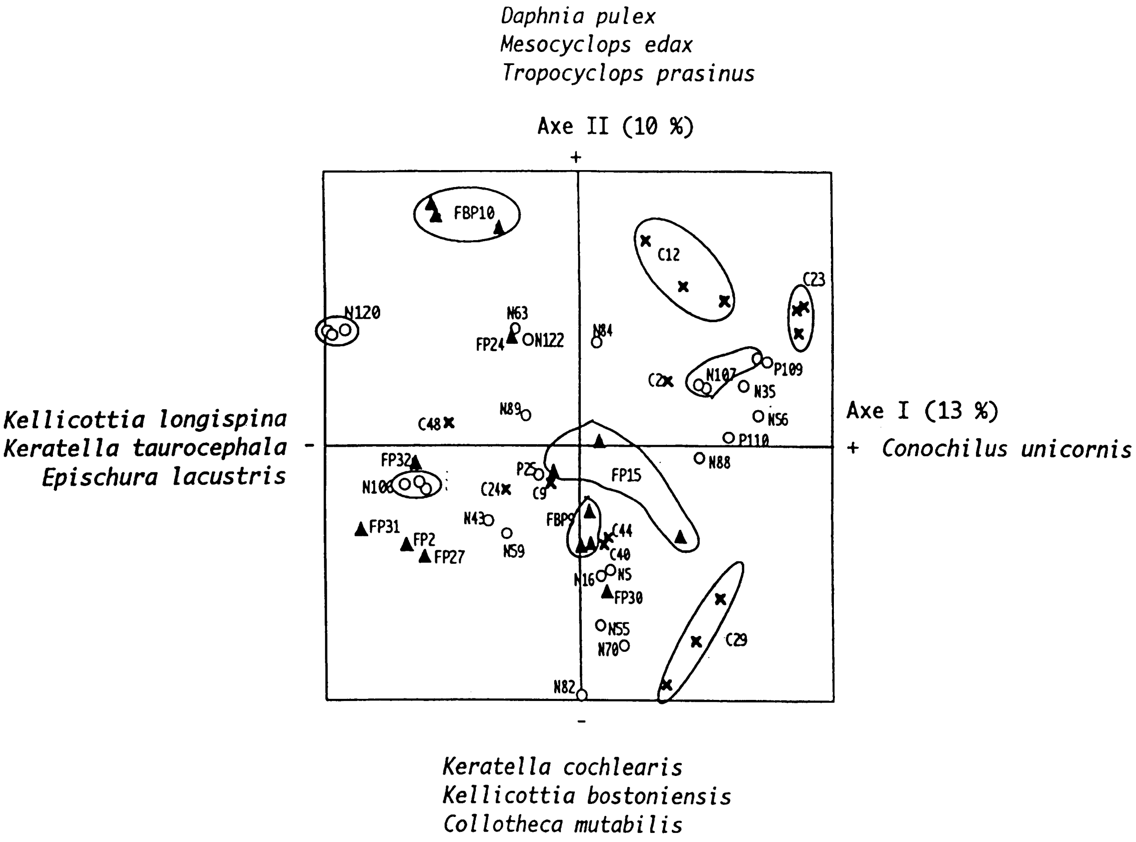


Figure 3. Clustering of lakes (n =38) and sampling replicates in 9 lakes (in circles), in the first PCA ordination plan based on the similarity of species assemblages in lakes in each group (reference, logged, burned) in July 1996. N or P refer to the reference lakes, C to the logged lakes, and F to the burned lakes. Discriminant species correlated with the PCA axes are listed on each side of the ordination plan.

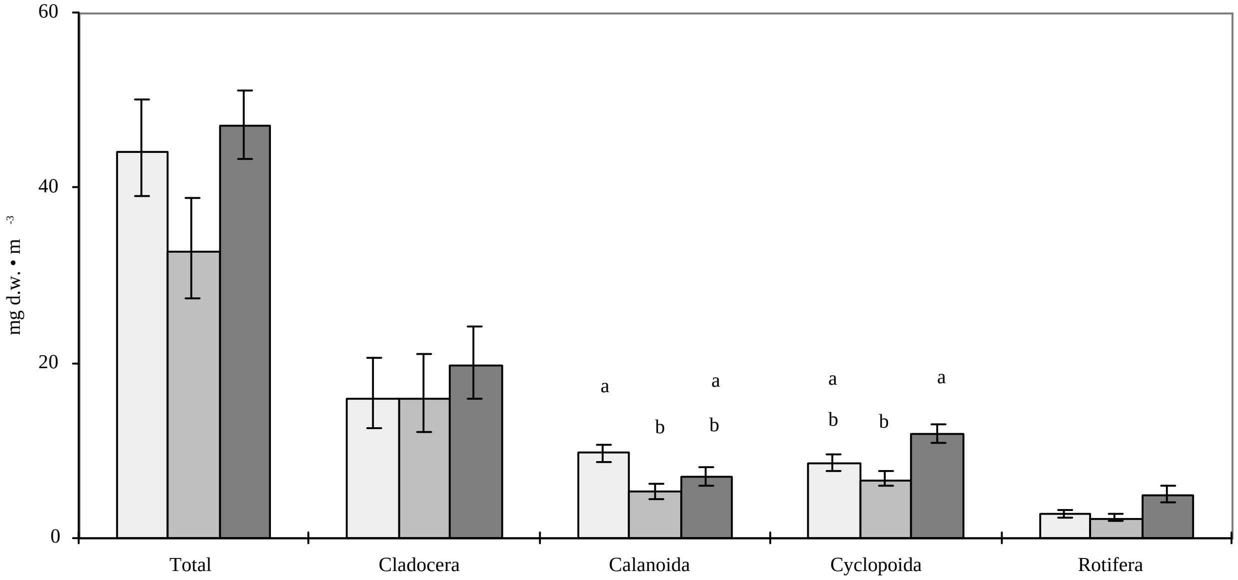


Figure 4. Among-group differences in the 1996 mean biomass of total zooplankton and taxonomic groups (mg d.w.•m^{-3}). From left to right, bars represent undisturbed- (light stippling), logged- (hatched) and burned-watershed lakes (shaded). Error bars represent one standard error. Bars with different letters represent groups with significantly different means (alpha=5%, Duncan multiple range test).

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 logged and burned 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.

Contrary to our expectations, there was a general tendency for logged-watershed lakes to support biomasses of zooplankton equivalent or lower (calanoids) to those of reference lakes (Fig. 4), despite higher TP concentrations (Table 1). When examining the absence of difference in zooplankton biomass between reference and logged-watershed 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 legislations require 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 logged-watershed lakes, thus in part accounting for the absence of detectable zooplankton biomass differences between logged-watershed and reference lakes.

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 other zooplankton groups, calanoid biomass was lower in logged 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 TN ($r = -0.4$, $P = 0.01$) 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.

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 lake over a three year period. Natural fires increase limnoplankton biomass in burned lakes, whereas logging never affect the biomass of limnoplankton in logged lakes (Fig. 5). Burned-watershed lakes supported 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 burned-watershed than in reference and logged-watershed lakes during the first year after disturbance. The highest increases in the biomass of total limnoplankton and size fractions occurred two years after disturbance. This increase in limnoplankton biomass 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), or Chl-*a* (Pace 1986) in North-American lakes.

It is interesting to note that burned-watershed 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 before the crustaceans. Crustaceans are known to express 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 planktivory pressure in the burned group of lakes (Brooks and Dodson 1965). Data on planktivore fish density, however, provide no indication of such among-group differences in planktivory pressure (Table 1).

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 environmental changes in boreal lakes following watershed disturbances.

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. 5). This indicates 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. 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 burned and logged lakes in 1998 (Carignan et al. 1999).

Sources of Variation

We assessed the relative importance of watershed conditions and sampling periods as sources of variation in zooplankton and limnoplankton biomass attributes based on the 1996 samples (Table 3). 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. 1999, submitted). 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 emphasizes 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.

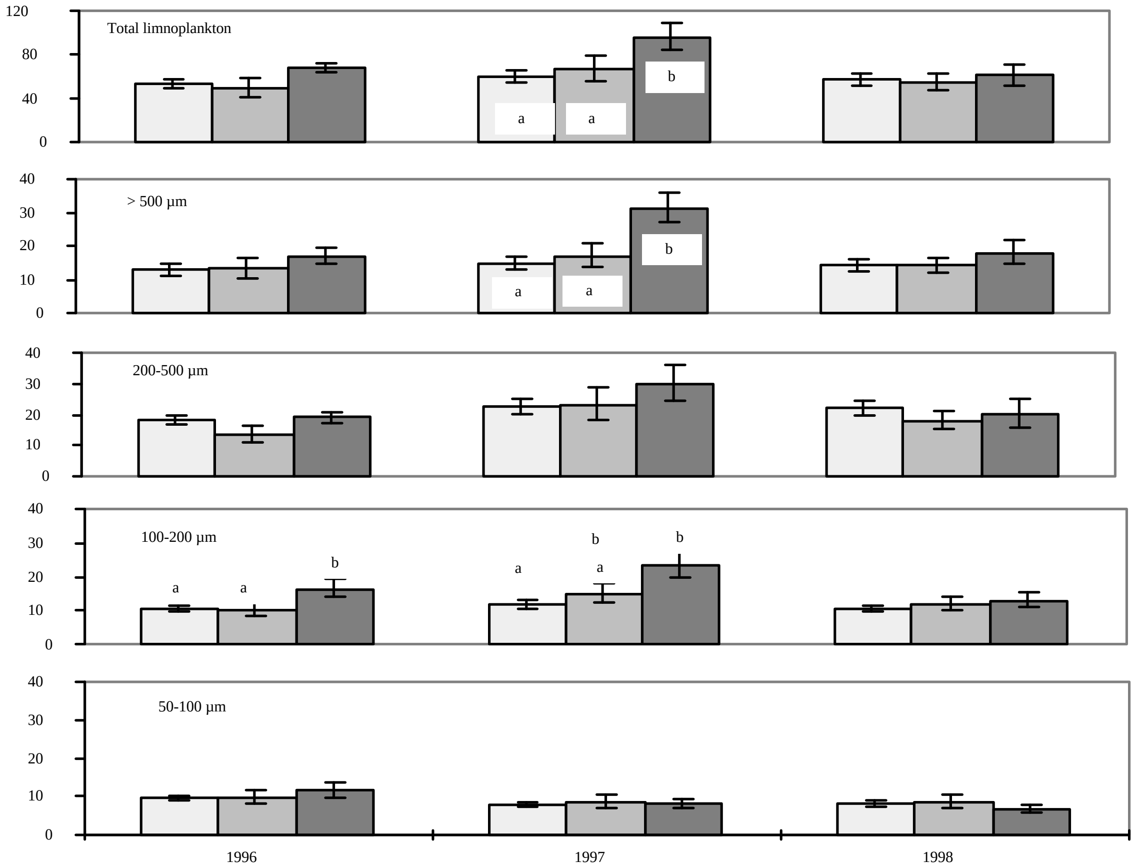


Figure. 5. Among-group differences in total limnoplankton and the four size fractions during the years 1996, 1997 and 1998 (mg AFDW•m^{-3}). From left to right, bars represent undisturbed- (light stippling), logged- (hatched) and burned-watershed lakes (shaded). Error bars represent one standard error. Bars with different letters represent groups with significantly different means (alpha=5%, Duncan multiple range test).

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 4). 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 consistantly 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 3. Relative importance of watershed condition and sampling period as factors accounting for the total variation in zooplankton biomass during the first year following watershed distrubance. 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%

Table 4. Pearson correlation coefficients between zooplankton biomass (total and taxonomic groups) and environmental variables for the 38 lakes in 1996. Correlations are based on loggeg 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 (µg L^{-1})	ns	ns	ns	ns	0.41*
TN (µg 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 *a* (µg 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 5). Among the water quality variables, TP, TN and Chl-*a* were significant correlates of total limnoplankton and the 100-200 µm and > 500 µm 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 µm size fractions; these were positive and restricted to the first year. Piscivorous density was positively correlated with the > 500 µm 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*.

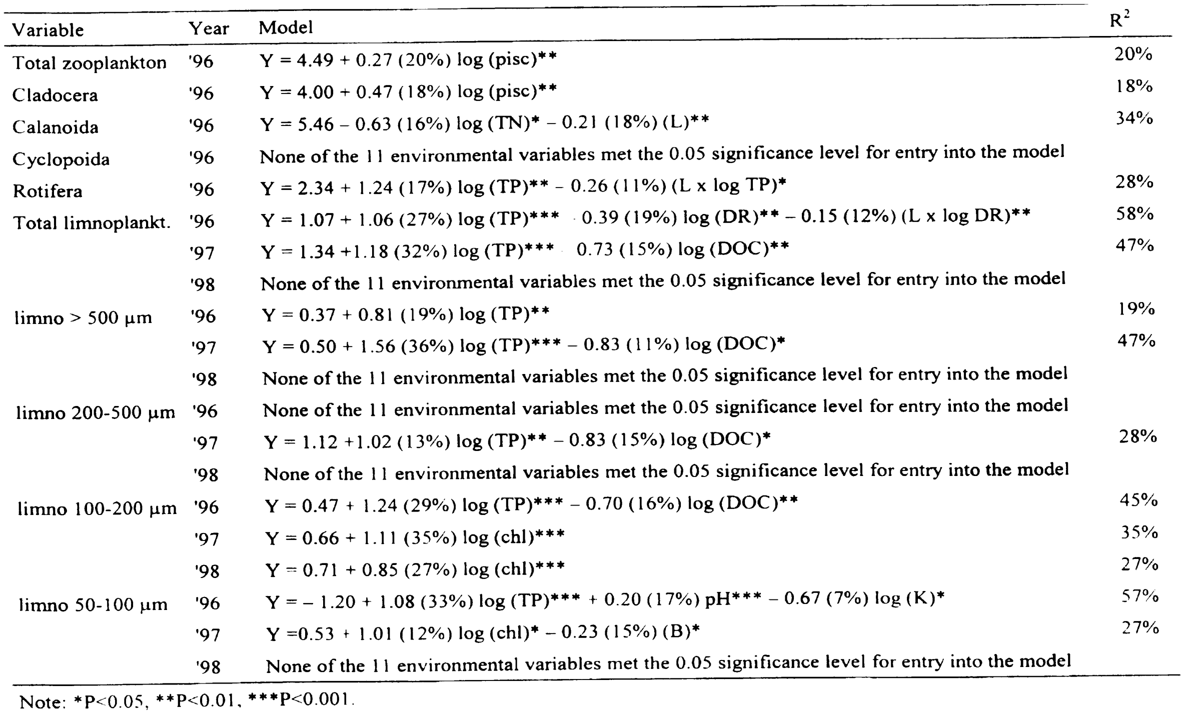
Table 5. Pearson correlation coefficients between limnoplankton biomass (size fractions and total limnoplankton) and environmental variables of the 38 lakes during 1996, 1997, and 1998. The year of the data on which the correlation is based is indicated in parenthesis. Correlations are based on logged 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 (µg•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 (µg•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+ (µg•L-1)	+0.34* ('96) +0.38* ('97)	+0.38* ('96) +0.48** ('97)	ns	+0.38* ('96) +0.37* ('97)	ns
DOC (mg•L-1)	ns	ns	ns	ns	ns
Chlorophyll *a* (µg•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.•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 ($P > 0.05$); * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 6 displays the regression models that were developped for the zooplankton and limnoplankton variables, using the environmental variables that showed the highest significant correlation coefficients (Tables 4 and 5). No model was developped for cyclopoids because none of the environmental variables examined correlated significantly with cyclopoid biomass. In all cases, the coefficients of determination (r^2) dit 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 color 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 6. 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	$Y = 5.46 - 0.63\ (16\%)\ \log(\text{TN})^{*} - 0.21\ (18\%)\ (\text{L})^{**}$	34%
Cyclopoida	'96	None of the 11 environmental variables met the 0.05 significance level for entry into the model	
Rotifera	'96	$Y = 2.34 + 1.24\ (17\%)\ \log(\text{TP})^{**} - 0.26\ (11\%)\ (\text{L} \times \log \text{TP})^{*}$	28%
Total limnoplankt.	'96	$Y = 1.07 + 1.06\ (27\%)\ \log(\text{TP})^{***}\ \ 0.39\ (19\%)\ \log(\text{DR})^{**} - 0.15\ (12\%)\ (\text{L} \times \log \text{DR})^{**}$	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	$Y = 0.53 + 1.01\ (12\%)\ \log(\text{chl})^{*} - 0.23\ (15\%)\ (\text{B})^{*}$	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 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 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 burned 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 burned-watershed 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-watershed lakes in 1996. This was in fact supported by preliminary length frequency data for yellow perch and lake whitefish (Magnan and Saint-Onge 1999). If DOC can be shown to be responsible for this decrease in calanoid and cyclopoid biomass - as data herin 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 burned-watershed 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 burned-watershed lakes. This variation in total zooplankton biomass was that of an increase in burned-watershed lakes, that reach 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 burned lakes is linked to higher nutrient inputs from watershed and higher algal biomass. In contrast the lack of effect or the negative impact of loggin 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. 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 burned lakes. Negative impact of logging are related to increase in water color and divolved 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 seasonality, watershed physiography and lake conditions. The extent od watershed disturbances either by fire or logging should be important (> 50% of the watershed area) to have important impact on lake plankton.

Future analyses will compare the impacts of natural fire and logging at long term on the dominant zooplankton species and size spectra. It is hoped that these approaches will be more successful in showing patterns with environmental variables (and hence watershed conditions) than was the broad approaches based on zooplankton group or size fractions.

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