

Short-term impact of forest harvesting on water quality and zooplankton communities in oligotrophic headwater lakes of the eastern Canadian Boreal Shield

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The objective of this study was to investigate the short-term impact of forest harvesting within the first year after perturbation on water quality and zooplankton in oligotrophic lakes of the eastern Canadian Boreal Shield. To achieve this objective a balanced multiple before/after-control-impact (MBACI) experimental design was used including four headwater lakes sampled twice before (July and September 2003) and twice after harvesting (July and September 2004) and four undisturbed control lakes sampled at the same dates. Significant increases in dissolved organic carbon (DOC) and total phosphorus (TP) concentrations were detected after the perturbation but did not result in a bottom-up effect. Differences in pelagic phytoplankton biomass and zooplankton community structure were not related to harvesting activities. Spatial and temporal variability was observed among lakes in logged as well as in control lakes. Therefore natural variability seemed to be more important in determining ecological patterns within the lakes than the short-term impacts of forest harvesting. We hypothesise that novel logging strategies such as careful logging around advanced growth in combination with 20-m buffer strips fringing streams and lakes might be an efficient protection to mitigate short-term effects of additional allochthonous matter input in lake pelagic zones after forestry activities on watersheds.

Introduction

In terrestrial ecosystems, forestry activity is known to have direct impacts on flora and fauna

through habitat alteration by logging, ditching and scarification, whereas the impact on aquatic systems is indirect. The impact of logging on lotic ecosystems is well documented (for review

see Smith *et al.* 2003, Feller 2005, Moore and Wondzell 2005, Moore *et al.* 2005), reporting an increase in runoff and a change in physico-chemical (Bourque and Pomeroy 2001, Ensign and Mallin 2001) and biological (Gregory *et al.* 1987) properties. Canopy removal induced a decrease in dissolved oxygen and increases in water temperature, nutrient loads and primary production (Sabater *et al.* 2000), that may consequently affect invertebrate (Herlihy *et al.* 2005, Nislow and Lowe 2006) and fish (Nislow and Lowe 2003, 2006, Baldigo *et al.* 2005) communities.

There is much less information available on effects of forestry activity on lentic ecosystems. In lakes, the few short-term impact studies of forest harvesting and wildfire reported slight eutrophication as revealed by an increase of dissolved organic carbon (DOC) concentration that changed the light regime of the euphotic zone (Rask *et al.* 1998, Carignan *et al.* 2000) and an increase in nutrient loads that consequently lead to higher primary production (Planas *et al.* 2000). In contrast, increased DOC and phosphorus loading resulted in nitrogen limitation, light limitation and a decrease of phytoplankton species richness in boreal subarctic lakes in peatland environments after forest fires (McEachern *et al.* 2002). No impact of harvesting was found on diversity, size spectra and species assemblages of zooplankton communities (Pinel-Alloul *et al.* 1998, Patoine *et al.* 2002a, 2002b), but a negative impact was reported on biomass of calanoid copepods (Patoine *et al.* 2000) and on juvenile fish abundance (St-Onge and Magnan 2000). These negative effects seemed to be contradictory given the fact that the increase of phytoplankton should favour zooplankton nutrition, reproduction and availability to larval and juvenile fish. The effects on zooplankton seemed to extent no longer than two years (Patoine *et al.* 2000). In general zooplankton communities were very stable in boreal lakes and had strong resilience to perturbations by wildfires and clear-cut logging (Jalal *et al.* 2005). Using a paleolimnological approach evaluating forestry impact on a ten-year scale, diatom communities changed over time whether harvesting occurred or not (Laird and Cumming 2001, Laird *et al.* 2001) and subtle changes in cladoceran species

composition followed forest logging (Bredesen *et al.* 2002). Impacts of harvesting and wildfires on lentic fish assemblages in the Boreal Plains of Alberta over a 1 to 2 year time period were small, showing a slight increase of white sucker that reflected a modest enrichment effect in burned lakes (Tonn *et al.* 2003).

Many studies mentioned above could not dissociate effects of harvesting activities and wildfire. The impact of harvesting was always minor as compared with the impact of natural disturbances such as wildfires on catchments of headwaters (Jalal *et al.* 2005, Pinel-Alloul *et al.* 2002, Nitschke 2005). However, largest impacts on lakes were documented due to deforestation with subsequent urbanization ultimately changing the trophic status of a lake (Wolin and Stoermer 2005).

Modification of landscape by harvesting will certainly continue to increase, so that forest management practices that allow sustainable resource harvesting are becoming an important issue (Nitschke 2005). Due to results of impact studies, logging practices have changed from total harvesting by clearcut to less severe strategies such as careful logging around advanced growth (CLAAG also known as CPRS in Quebec) and partial/selection harvesting. For example, the CLAAG strategy preserves all stems smaller than 10 cm in diameter and minimise soil perturbation (Bérard and Côté 1996). In addition, riparian buffer strips appear to be useful in reducing short-term impacts of clearcutting, though they do not eliminate these impacts altogether (Miller *et al.* 1997, Moore *et al.* 2005).

Most of the short-term impact studies of catchment harvesting on lakes did not evaluate the variability of the aquatic system prior to the perturbation, with the exception of Rask *et al.* (1998) that investigated a single control lake, with the risk of including spatial confounding factors (Underwood 1992). A solution to the problem of confounding factors is to measure the natural interactions before and after impact in lakes that are not logged (i.e. in several control lakes) and to contrast this with the interaction between logged and control lakes (Underwood 1992, Keough and Mapstone 1995). Bennett and Adams (2004) pointed out that inappropriate interpretation of results from non-replicated

experimental design remains an ongoing issue. A MBACI (multiple before/after-control-impact) design, described by Keough and Mapstone (1995), was used in this study.

The objective of this study was to investigate the short-term impacts of forest harvesting within the first year after perturbation on water quality and zooplankton in oligotrophic lakes of the eastern Canadian Boreal Shield by comparing various limnological characteristics from these lakes before and after the perturbation in their catchment and comparing these with undisturbed control lakes. More specifically, the null hypothesis was that logging activities will not modify water quality (dissolved organic carbon, total phosphorus and total nitrogen) and zooplankton community characteristics (biomass, abundance, species richness, diversity and evenness) in eastern Canadian Boreal Shield lakes. To achieve this objective we chose a balanced multiple before/after-control-impact (MBACI) experimental design including four headwater lakes sampled twice before and twice after the logging activity and four undisturbed control lakes sampled on the same dates. This approach allowed us to separate changes due to logging from natural variability, because the latter should also be found in the undisturbed control lakes. As suggested by Bennett and Adams (2004) this approach would greatly benefit the urgent need to measure the environmental impacts of human activities accurately. This study is the first of several studies, being part of a broad project evaluating the impacts of logging on oligotrophic lakes, investigating water characteristics and plankton, benthic and fish communities.

Methodology

Study area and sampling sites

The lakes examined in this study were located in the province of Quebec, on the Boreal Shield near Lake Mistassini (between 50°15'N, 73°30'W and 50°45'N, 72°30'W, Fig. 1). This region is dominated by virgin black spruce (*Picea mariana*) forests. The soil layer over the rock is thin and the lakes in this region are oligotrophic. First- and second-order lakes were selected to

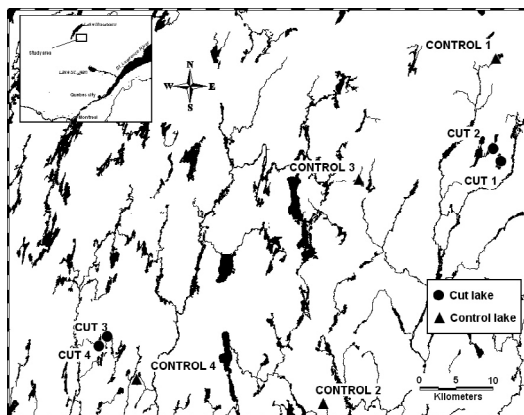


Fig. 1. Location of cut and control lakes sampled in 2003 and 2004.

evaluate the most direct impact of harvesting. Lake surface ranged from 0.38 to 1.09 km² (Table 1). Their catchment area varied from 1.19 to 4.23 km² (Table 1) and was composed for the most part of mature black spruce stands. Mean slope in the catchments ranged from 4.97% to 13.11% (Table 1). Precipitation, geology and vegetation were similar within the study area. As proposed by Duhaime and Pinel-Alloul (2005), a multivariate procedure was used to evaluate if cut lakes and control lakes have similar limnological characteristics. No significant difference was found between the two types of lakes using 17 geographical and limnological variables measured before perturbation (altitude, latitude, longitude, maximum depth, lake area, shoreline development, catchment area, catchment mean slope, mean secchi depth, mean temperature in the euphotic zone, mean surface pH, mean dissolved oxygen in the euphotic zone, mean surface conductivity, total nitrogen, total phosphorus, dissolved organic carbon and chl *a*; Table 1; $p = 0.09$; Permutational analysis of variance on Bray-Curtis similarity matrix, ANOSIM procedure, PRIMER ver. 6 statistical package, Bray and Curtis 1957, Clarke and Warwick 2001). Forest was cut using the careful logging around advanced growth (CLAAG) strategy and 20-m strips of standing forest was kept along lakes and streams after harvesting activities. All cut lakes correspond to the impact criteria of a drainage ratio higher than 4 (Carignan *et al.* 2000) and a percentage of catchment area cut higher than 40% (Pinel-Alloul *et al.* 2002; Table 1).

Table 1. Lake characteristics of the eight studied Canadian Boreal Shield lakes. Catchments of four lakes have been harvested in autumn 2003/winter 2004 (Cut-1–Cut-4) and catchments of four control lakes remained undisturbed (Control-1–Control-4). Secchi depth, temperature, pH, dissolved oxygen (DO) and conductivity are reported as means (SD) over the sampling dates before the perturbation (July and September 2003).

Lake characteristics	Cut-1	Cut-2	Cut-3	Cut-4	Control-1	Control-2	Control-3	Control-4
Altitude (m)	492	499	478	478	504	468	513	482
Latitude N	50°33'48''	50°34'40''	50°20'56''	50°20'31''	50°41'19''	50°16'01''	50°32'19''	50°17'50''
Longitude W	72°33'30''	72°34'29''	73°18'30''	73°19'37''	72°33'45''	72°53'50''	72°49'44''	73°15'10''
Maximum depth (m)	9.76	10.08	12.55	9.00	10.90	10.46	24.01	14.52
Lake area (km ²)	0.71	0.88	0.42	0.38	1.09	0.39	0.59	0.52
Lake perimeter (km)	7.66	6.26	5.06	4.75	5.60	3.55	6.24	4.44
Fetch (km)	2.06	2.08	1.59	1.66	2.20	1.04	1.46	1.70
Shoreline development (km)	2.56	1.88	1.99	2.17	1.51	1.61	2.29	1.74
Catchment area (km ²)	4.23	3.70	2.96	1.67	3.82	3.95	2.53	1.19
Catchment perimeter (km)	12.43	14.29	9.37	7.36	11.04	11.97	8.17	6.80
Catchment mean slope (%)	6.59	6.21	8.19	4.97	5.40	13.11	5.70	6.57
Drainage ratio	5.92	4.18	7.12	4.37	3.50	10.15	4.27	2.29
Order	1	2	2	1	1	2	1	1
Lake volume (× 10 ³ m ³)	1835.194	3919.487	1931.606	n/a	4299.124	1384.988	3990.306	2957.841
Turn over rate (N per year)	1.24	0.92	1.01	n/a	0.52	1.45	0.36	0.27
Harvested area (% of catchment area)	57.1	65.2	50.6	40.4				5.1
Time of harvest	Autumn 2003	Autumn 2003	Winter 2004	Winter 2004				
Mean secchi-depth (m)	1.63 (0.14)	1.65 (0.16)	1.83 (0.36)	1.60 (0.44)	2.25 (0.27)	1.88 (0.14)	3.00 (0.00)	3.75 (0.00)
Mean temperature euphotic zone (°C)	15.75 (3.22)	16.12 (3.62)	15.49 (3.64)	15.70 (3.50)	15.60 (3.01)	15.05 (2.73)	15.30 (3.69)	15.59 (3.16)
Mean pH surface	6.37 (0.25)	6.43 (0.07)	6.51 (0.47)	6.75 (0.38)	6.54 (0.18)	6.78 (0.12)	6.91 (0.48)	6.94 (0.35)
Mean DO euphotic zone (mg l ⁻¹)	10.01 (1.11)	11.03 (0.89)	8.44 (1.09)	8.46 (1.10)	10.34 (0.87)	10.18 (1.04)	8.69 (1.05)	8.49 (1.14)
Mean conductivity surface (µS cm ⁻¹)	14.88 (0.33)	12.10 (0.44)	18.50 (0.00)	17.12 (3.41)	9.92 (0.47)	19.03 (1.30)	20.40 (0.00)	20.05 (0.00)

Experimental design

A MBACI (multiple before/after-control-impact; Keough and Mapstone 1995) model was used, including four lakes that were harvested after the first summer of sampling (harvested surface was 40%–65% of the catchment area) and four control lakes (no logging within the catchment). All lakes were sampled twice in summer 2003 (23–24 July and 3–9 September) before logging and twice in summer 2004 (22–28 July and 8–9 September) after the perturbation. Therefore, eight undisturbed lakes were sampled in 2003 (four future logged lakes and four control lakes), and four perturbed lakes (logged) and four undisturbed lakes (control) were sampled in 2004.

Water quality and chl *a*

Access to undisturbed lakes was only possible by seaplane which also served as a sampling platform. Samples were always taken in the pelagic part, near the deepest point of each lake. Temperature and dissolved oxygen (DO) profiles of the entire water column were measured using a multi-probe system (YSI 556 MPS). Three independent, integrated water samples were taken from the euphotic zone (estimated as: secchi depth $\times$ 1.25, according to observations on eastern Boreal Shield lakes by R. Carignan, Université de Montréal, pers. comm.). Water samples were stored at 4 °C during transport to Université de Montréal for analyses of dissolved organic carbon (DOC), total phosphorus (TP) and total nitrogen (TN) concentrations according to Carignan *et al.* (2000). Three additional samples of integrated water were taken at the same site for phytoplankton biomass estimation. Chl *a* was concentrated within 12 h by filtering 750–1000 ml of water through a Whatman GF/C filter. Chl *a* filters were immediately stored at –80 °C, kept in dark and were sent to Université du Québec à Montréal where extractions with hot 90% ethanol and absorbance measurements, before and after acidification, were performed according to Planas *et al.* (2000).

Zooplankton

Zooplankton was sampled at the same site by three independent vertical hauls made from 1 m off-bottom to the surface using a cantilevering net with a circular mouth opening of 0.25 m and mesh size of 53 μ m (Filion *et al.* 1993). Zooplankton was anaesthetized using carbonated water and then preserved in 4% buffered formaldehyde. In the laboratory, samples were first sorted to remove and count *Chaoborus* larvae (Chaoboridae, Diptera) separately, and then were divided into four equal fractions with a Folsom splitter; the first quarter was used for taxonomic analysis, the second quarter was used for biomass determination, and the two residual quarters were kept for further reference. Organisms were sub-sampled by aliquot using a pipette with a 4 mm opening and then identified to the lowest taxonomic level possible, usually to the species level using the following keys: Edmondson (1959) for general identification, Smith and Fernando (1978) for copepods, Hebert and Finston (1996, 1997) for *Daphnia*, DeMelo and Hébert (1994) for *Bosmina*, and Stemberger (1979) for rotifers identifications. A list of zooplankton taxa found in the lakes is given in the appendix. Biomass measurements of zooplankton, in mg of ash-free dry weight (AFDW) m^{-3} , were performed on decreasing size-fractions according to (Patoine *et al.* 2000). Samples were sieved through 500 μ m, 212 μ m, 116 μ m, and 53 μ m and then filtered onto precombusted GF/A glass fiber filters, dried for 18 h, weighed, ashed at 500 °C for 18 h and weighed again and the organic mass was calculated as the difference between dry weight and combusted weight.

Univariate statistical analyses

Balanced analyses of variance (ANOVAs, MBACI model) were performed on several measured variables including abiotic (DOC, PT, NT) and biotic parameters [Chl *a*, total zooplankton abundance (*N*), species richness (*S*), Shannon-Wiener diversity (*H'*), Pielou's evenness (*J'*), total zooplankton AFDW, zooplankton fractions AFDW (> 500 μ m, 212–500 μ m, 106–212 μ m, 53–106 μ m), and abundance of rotifers, *Daph-*

nia spp., *Bosmina* spp., calanoid copepods and cyclopoid copepods]. These taxa were selected in order to compare the results with those of other studies (Patoine *et al.* 2000, 2002a, 2002b, Planas *et al.* 2000). Furthermore, important prey items of larval and juvenile fish such as cyclopoid copepods, *Bosmina* spp. and *Daphnia* spp., were selected to investigate whether logging has an impact on the food source of young fish that could lead to bottom-up effects in the trophic web. The MBACI model had four factors, treatment (cut/control, fixed factor), lake within the treatment (random factor), periods before/after (fixed factor), survey within periods before/after (before: 3 July, 3 Sep./after: 4 July, 4 Sept., fixed factor) and their interactions (*see* Keough and Mapstone 1995, and Downes *et al.* 2002 for a complete description of the model; *see* Table 2). Data were transformed to achieve normality and homogeneity of variance when necessary (details given in Table 2 where appropriate). The principal source of variation of interest for impact assessment is the interaction between the treatment (cut/control) and the periods before/after. When a source of variation was significant ($p < 0.05$), a LSD (Least Significant Difference) pair-wise multiple comparison test were used to identify the differences.

Multivariate statistical analyses

Differences in the structure of the assemblages between treatments and dates were evaluated by non-metric multi-dimensional scaling (nMDS) ordination on fourth-root transformed data (abundance data), using the Bray-Curtis similarity measure (Bray and Curtis 1957, Clarke 1993). The same MBACI model (*see* univariate statistical analysis) was used to test for differences in zooplankton assemblages. This analysis was done using a permutational multivariate analysis of variance (PERMANOVA ver. 1.6, Anderson 2001, McArdle and Anderson 2001, Anderson 2005). This analysis had the same structure as the univariate MBACI model described above but it uses permutations to determine distributions of test-statistics. Data were fourth-root transformed and the Bray-Curtis dissimilarity was used. Number of permutations used was 4999.

Results

Water quality and chl *a*

A significant interaction between treatments and the periods before/after was observed for DOC and TP concentrations. The DOC ranged from 7.9 to 13.1 mg l⁻¹ in logged lakes and from 4.1 to 8.8 mg l⁻¹ in control lakes and was significantly higher in the logged lakes over the entire study. Nevertheless, a significant increase was observed after harvesting in 2004 in the four logged lakes, whereas the DOC levels stayed the same in the four control lakes (Fig. 2 and Table 2). The concentration of TP increased in the cut lakes while it decreased in the control lakes in 2004, after the perturbation (Fig. 2). The values of TN did not differ significantly between treatments and the periods before/after, hence no impact of logging could be detected (Table 2).

Chl *a* values showed similar pattern in logged and control lakes over time. No significant change due to perturbation was found following harvesting (Table 2). Changes in chl *a* were related to inter-annual variability, with higher values in 2003 than in 2004 (Fig. 3).

Zooplankton

Total abundance of zooplankton varied between years showing highest abundance in 2004 in both lake types. No significant difference was found between treatments (Table 2). Mean species richness ranged between 14.8 and 17.1 taxa over the study period and no difference was detected between logged and control lakes, but the ANOVA showed significant differences among lakes within treatment, showing high inter-lake variability (Fig. 3 and Table 2). No statistical significant interaction was found between treatment the periods before/after for the Shannon-Wiener diversity and Pielou's evenness (Table 2). However, there seemed to be a slight tendency that the mean Shannon-Wiener diversity and mean Pielou's evenness decreased after the harvesting impact in 2004 in the logged lakes, whereas in control lakes no change occurred (Fig. 3).

Similar patterns of total zooplankton biomass (total AFDW) were observed between logged

Table 2. Results of the three-way ANOVAs testing the effect of treatment (tr: cut, control), lake (la), periods before/after (b/a: 2003, 2004), survey (su: July, September) and their interactions on dissolved organic carbon (DOC), total phosphorous (TP), total nitrogen (TN), Chl *a*, zooplankton total abundance, species richness (S), Shannon diversity (H'), evenness (J), total ash free dry weight (AFDW), zooplankton biomass of size classes: > 500 µm, 212–500 µm, 106–212 µm and 53–106 µm, abundance of rotifers, Daphnia spp., Bosmina spp., cyclopoid and calanoid copepods, and results of the PERMANOVA on the entire zooplankton assemblage. Note that some variables were transformed.

Variable	df	tr	la(tr)	b/a	su(b-a)	tr × b/a	tr × su(b/a)	b/a × la(tr)	su(b-a) × la(tr)	Residual
Ln DOC	MS <i>p</i>	1 4.4666 0.0279	6 0.5367 < 0.0001	1 0.1141 0.135 0.2049	2 0.0153 0.1672 0.3019	1 0.2369 0.0473 0.697	2 0.0087 0.3388 0.0743	6 0.0383 0.0074 0.0772	12 0.0074 0.0045 0.0996	64 0.0027 0.0417
Ln TP	MS <i>p</i>	1 3.8669 0.033	6 0.5089 < 0.0001	1 0.1543 0.0314	2 0.0859 0.0842	1 0.0238 0.0266	2 0.4948 0.0153	6 0.6047 0.0383	12 0.0128 0.0268	64 0.021
Ln TN	MS <i>p</i>	1 1.8366 0.0109	6 0.1389 < 0.0001	1 0.4 3.7367	2 0.0799 0.9081	1 0.4366 0.1946	2 0.5792 0.1238	6 0.2811 1.9925	12 0.2534 0.6009	64 0.0413
Chl <i>a</i>	MS <i>p</i>	1 0.5763 0.5226	6 1.2508 < 0.0001	1 3.7367 0.2199	2 0.9081 0.2598	1 0.4366 0.7652	2 0.5792 0.8167	6 1.9925 0.0366	12 0.2534 < 0.0001	64 0.0413
Ln Total abundance + 1	MS <i>p</i>	1 0.7829 0.5819	6 2.3129 < 0.0001	1 5.0849 0.0328	2 1.2228 0.3956	1 0.5732 0.3898	2 1.8131 0.2649	6 0.6673 0.7634	12 1.2194 < 0.0001	64 0.0905
Species richness (S)	MS <i>p</i>	1 16.6667 0.3596	6 16.9444 0.0005	1 1.0417 0.782	2 14.7708 0.1859	1 5.0417 0.5477	2 6.1042 0.4708	6 12.4306 0.2206	12 7.6042 0.0294	64 3.625
Shannon diversity (H')	MS <i>p</i>	1 0.1493 0.5821	6 0.4418 < 0.0001	1 0.0923 0.6606	2 0.1827 0.6267	1 0.2653 0.4638	2 0.3851 0.3884	6 0.4334 0.3911	12 0.376 < 0.0001	64 0.0266
Ln Evenness (J) + 1	MS <i>p</i>	1 0.0017 0.7624	6 0.0174 < 0.0001	1 0.0056 0.6337	2 0.0183 0.3622	1 0.0107 0.5125	2 0.0144 0.4437	6 0.0222 0.3133	12 0.0166 < 0.0001	64 0.0011
Ln Total AFDW	MS <i>p</i>	1 6.0026 0.1028	6 1.6226 < 0.0001	1 1.0472 0.4552	2 1.6707 0.1782	1 0.0101 1.5538	2 0.3498 0.1345	6 1.6437 1.3025	12 0.836 0.0018	64 0.2721
Ln > 500 µm	MS <i>p</i>	1 0.2783 15.4645	6 3.9098 < 0.0001	1 0.1167 1.65715	2 4.3514 0.0811	1 0.94 0.3166	2 0.6674 0.9087	6 0.1502 0.5055	12 0.0001 < 0.0001	64 0.0971
Ln 212–500 µm	MS <i>p</i>	1 0.0464 0.91497	6 2.47141 < 0.0001	1 0.3729 3.77254	2 0.02364 0.9651	1 0.31507 0.6893	2 0.02487 0.9634	6 1.78795 0.0681	12 0.66429 < 0.0001	64 0.10061
Ln 106–212 µm	MS <i>p</i>	1 0.499 3.87521	6 1.76848 < 0.0001	1 0.058 3.18646	2 0.53534 0.3866	1 0.00031 0.9838	2 0.16181 0.7383	6 0.68986 0.3178	12 0.51984 < 0.0001	64 0.09053
Ln 53–106 µm	MS <i>p</i>	1 0.1763 0.4199	6 1.65038 < 0.0001	1 0.001 7.3186	2 0.8275 1.6514	1 0.4173 1.6773	2 0.9007 3.4359	6 0.08949 0.9914	12 0.0001 2.4024	64 0.09587
Ln Rotifers	MS <i>p</i>	1 0.7459 10.1767	6 3.6461 < 0.0001	1 0.165 7.8856	2 0.5216 1.2629	1 0.1658 1.652	2 0.2773 0.127	6 0.9353 0.2846	12 < 0.0001 0.3645	64 0.0859
Ln Daphnia spp. + 1	MS <i>p</i>	1 0.0199 6.228	6 1.0278 < 0.0001	1 0.0019 0.117	2 0.0649 1.2586	1 0.0526 0.2259	2 0.7128 1.4352	6 0.6008 1.7326	12 < 0.0001 0.783	64 0.1658
Ln Bosmina spp. + 1	MS <i>p</i>	1 0.6663 1.5836	6 1.2408 < 0.0001	1 0.8037 0.3047	2 0.2407 0.1889	1 0.0526 0.7304	2 0.7128 0.202	6 0.6008 1.139	12 < 0.0001 0.6163	64 0.2663
Ln Cyclopoid copepods + 1	MS <i>p</i>	1 0.1901 14.466	6 0.7257 0.0202	1 0.5123 1.0739	2 0.7416 0.4975	1 0.5706 1.0238	2 0.3344 0.4295	6 0.4577 2.4875	12 0.0159 0.6603	64 0.2811
Ln Calanoid copepods + 1	MS <i>p</i>	1 0.1449 5219.3099	6 5.1538 < 0.0001	1 0.5355 7493.3601	2 0.4917 6954.7695	1 0.5449 3752.1885	2 0.5392 3955.5834	6 0.0241 3147.4277	12 0.0144 3490.337	64 2827.6401
Zooplankton assemblage	MS <i>p</i>	1 0.354 5219.3099	6 4504.946 0.001	1 0.009 7493.3601	2 0.0018 6954.7695	1 0.2974 3752.1885	2 0.2842 3955.5834	6 0.2154 3147.4277	12 0.0268 3490.337	64 2827.6401

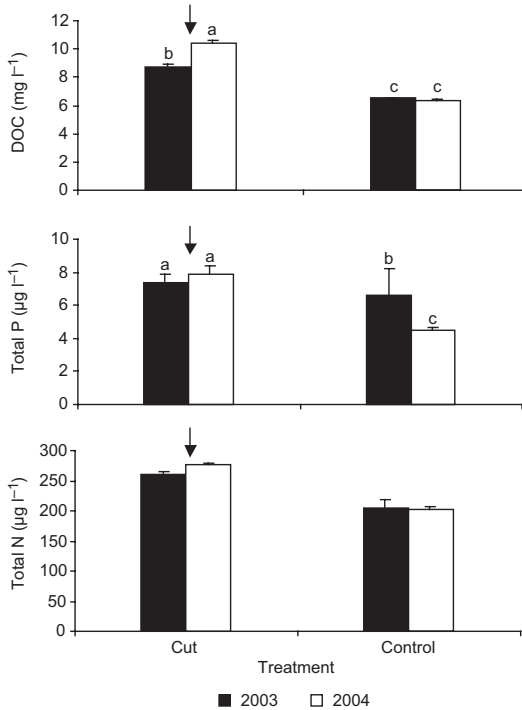


Fig. 2. Comparison between treatments (cut, control) and periods before/after (2003, 2004) of dissolved organic carbon (DOC), total phosphorous (TP) and total nitrogen (TN). Arrow indicate harvesting in autumn 2003–winter 2004. Vertical bars represent standard errors. Different letters (a–c) demonstrate significant differences (LSD, $p < 0.05$), similar letters demonstrate statistical similarity.

and control lakes. Increasing the resolution by splitting total biomass in four size fractions to verify if different size classes might be more vulnerable to harvesting than others showed no significant interaction between treatments and the periods before/after in either of the fractions (Fig. 4 and Table 2).

None of the selected zooplankton taxa showed significant differences in abundance regarding the interaction between treatments and the periods before/after (Table 2). Abundance of rotifers and *Daphnia* spp. showed similar pattern in logged and controls lakes with higher abundance in 2004 than 2003 in both type of lakes. *Daphnia* spp. abundance tended to be higher in logged lakes than in control lakes after harvesting ($p = 0.0526$; Fig. 5 and Table 2). Changes in *Bosmina*

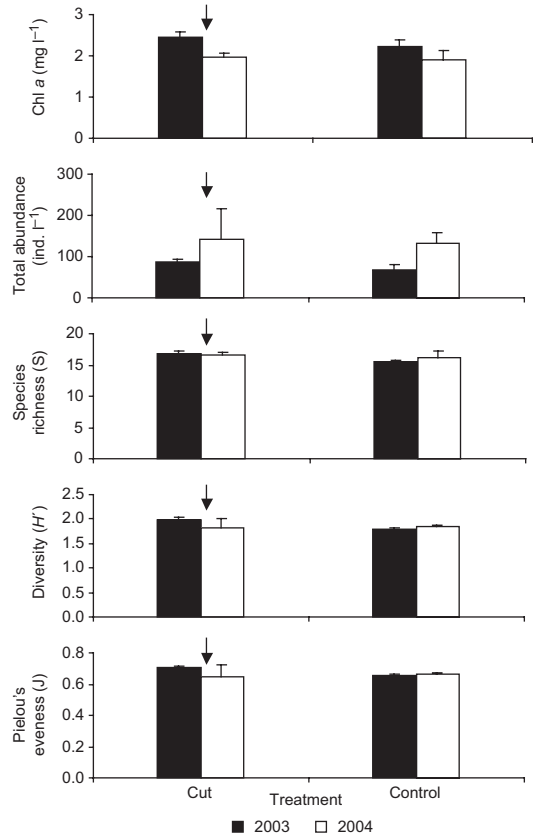


Fig. 3. Comparison between treatments (cut, control) and periods before/after (2003, 2004) of Chl a, and zooplankton total abundance, species richness, Shannon diversity index and Pielou's evenness. Arrow indicate harvesting in autumn 2003–winter 2004. Vertical bars represent standard errors.

spp., cyclopoid and calanoid abundances over time and treatment were not significant (Fig. 5 and Table 2).

Comparison of zooplankton assemblages by permutational multivariate analysis of variance (PERMANOVA) revealed no significant interaction between treatments and the periods before/after (Table 2). Likewise, the nMDS ordination comparing zooplankton assemblages of logged and control lakes before and after the perturbation showed no evidence of difference (Fig. 6). Distribution of symbols of logged and control lakes were scattered and interspersed suggesting no important impact of harvesting on the zooplankton assemblage in logged lakes.

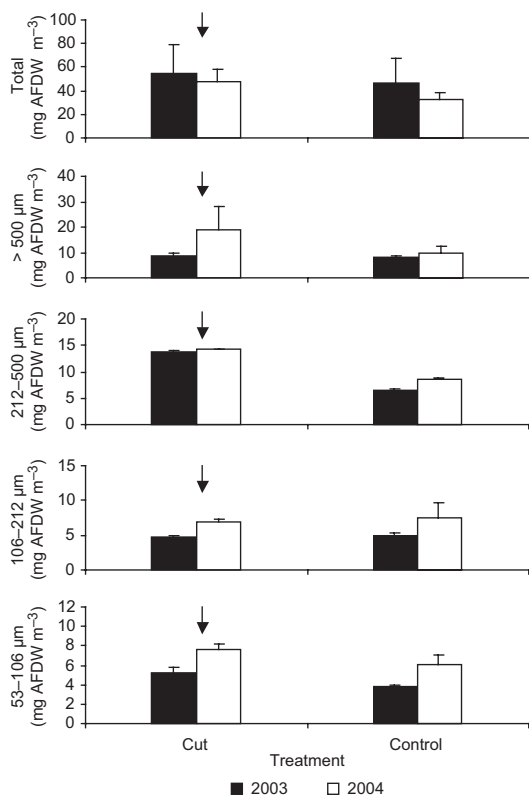


Fig. 4. Comparison between treatments (cut, control) and periods before/after (2003, 2004) of total zooplankton biomass (total AFDW) and of > 500 µm fraction AFDW, 212–500 µm fraction AFDW, 106–212 µm AFDW and 52–106 µm AFDW. Arrow indicate harvesting in autumn 2003–winter 2004. Vertical bars represent standard errors.

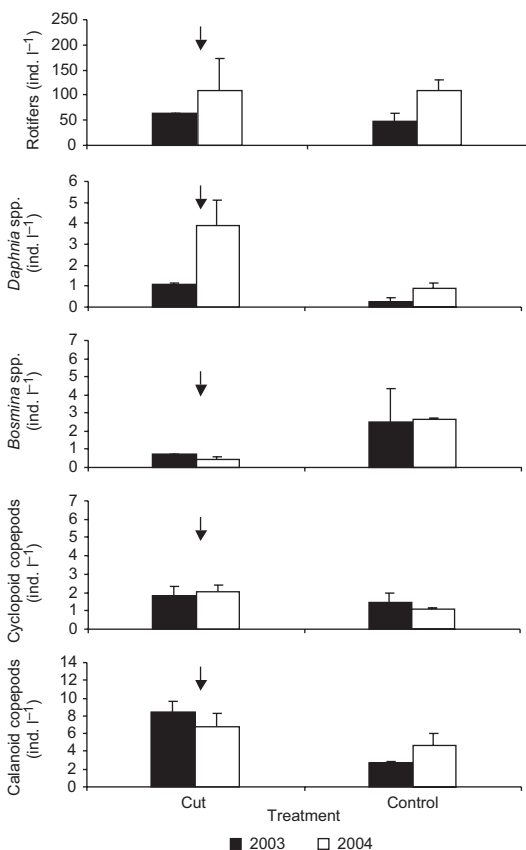


Fig. 5. Comparison between treatments (cut, control) and periods before/after (2003, 2004) of the abundance of rotifers, *Daphnia* spp., *Bosmina* spp., cyclopoid and calanoid copepods. Arrow indicate harvesting in autumn 2003–winter 2004. Vertical bars represent standard errors.

Discussion

Water quality and chl *a*

DOC increased significantly after harvesting in logged lakes compared to control lakes suggesting that the increase is mainly due to allochthonous material washed into the lakes after snowmelt in spring 2004. This allochthonous carbon source can serve as carbon and nutrient subsidies for bacterioplankton (Arvola *et al.* 1996, Carpenter *et al.* 2005, Lennon and Pfaff 2005). These authors showed that bacterial metabolism is influenced by the nature of dissolved organic matter (DOM) source and carbon specific bacterial production is related

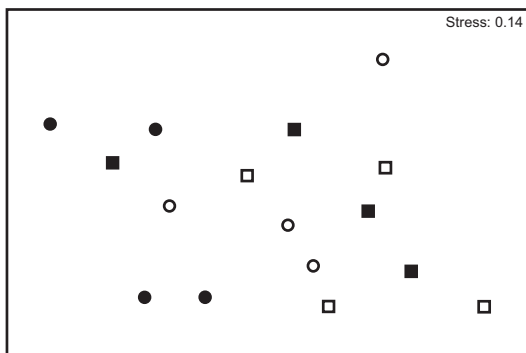


Fig. 6. Non-metric multidimensional scaling (nMDS-plot) on the entire zooplankton assemblage, comparing treatments, cut (squares) and control (circles) and periods before/after, 2003 (black) and 2004 (white) for all sampled lakes.

to C:P ratios of different DOM sources. No measurement on bacterioplankton was taken in this study. However, one would expect a bottom-up effect to higher trophic levels as shown in several studies. Pace *et al.* (2004) showed in a whole-lake experiment that aquatic food webs are supported to great extent by allochthonous carbon sources. Rotifers and *Daphnia* spp. are known to be effective grazers of protists and bacteria linking bacterial production directly to a higher trophic level of metazooplankton (Pace and Cole 1994, Sanders *et al.* 1994, Langenheder and Jürgens 2001). Assuming that rotifers and cladocerans take advantage of an increase in food availability, their secondary production may also augment. However, our results did not show any increase in density or biomass for these taxa, which may be due to a top-down control effect of planktivorous predators such as fish. Top-down control by fish on zooplankton has been reported in several studies in lakes (Ramcharan *et al.* 1995, 1996, Carpenter *et al.* 2001).

Increase in DOC also affects the light regime within a lake resulting in a shallower euphotic zone. Thus reduced light penetration may decrease primary production if it was not nutrient limited before, which is usually the case in oligotrophic lakes (Petersen *et al.* 1997). Therefore reduced light penetration may have little effect on primary production in the pelagic zone. Furthermore we have detected an increase in TP concentration but not in TN concentration in the pelagic zone after harvesting. Lamontagne *et al.* (2000) found increased export of TP and TN in runoff from catchment after harvesting, resulting in supplementary inputs to lakes and higher concentrations of these nutrients in the littoral zone. This was supported by findings of a larger increase in benthic algal and periphyton growth in the littoral zone than in pelagic algal growth after perturbation such as logging or wildfires (Rask 1998, Planas *et al.* 2000). The littoral zone may be a good buffer zone, utilizing and retaining the imported nutrients up to a certain level after perturbation, increasing its production and diminishing nutrient loads immediately before they might reach the pelagic zone (Loeb *et al.* 1983, Scheffer *et al.* 1993).

Given that DOC concentration modified light

conditions after logging, one would expect a decrease in primary production. However, pelagic algal response to catchment perturbation measured as chl *a* could not be detected in the first summer after harvesting in accordance to Rask *et al.* (1998). This suggests that the increase in TP concentration have balanced the light limitation due to higher DOC concentration. In contrast, higher chl-*a* concentrations together with higher nutrient loads and DOC concentrations were found in harvested or burned lakes compared to control lakes in the first year after perturbation by a previous study on the eastern Canadian Boreal Shield (Planas *et al.* 2000). But similarly to the present study, Planas *et al.* (2000) did not show evidence of bottom-up effects which are known to be more important at lower trophic levels and attenuated from one level to another (McQueen *et al.* 1986).

Zooplankton

Total abundance and total biomass of zooplankton were similar in disturbed and in control lakes the year after the perturbation event confirming the observation of Pinel-Alloul *et al.* (1998) and Patoine *et al.* (2000). Furthermore none of the four biomass size classes in our study showed significant effect of harvesting in accordance with the results of Patoine *et al.* (2000). However, these authors showed a significant decrease in calanoid biomass after perturbation compared to control lakes suggesting the increase in nutrient levels as a potential cause for this decrease. Calanoid copepods are often associated with nutrient-poor environments (Pace 1986) and might be less competitive than cyclopoid copepods under elevated nutrient levels. Species biomass and richness increased only in short life-span and r-strategic species such as rotifers over a 2 and 3 year survey period, respectively, in perturbed lakes as compared with those in control lakes (Jalal *et al.* 2005). The increase was significant in wildfire lakes as compared with that in control lakes, whereas clear-cut lakes had an intermediate position in between wildfire and control lakes (Jalal *et al.* 2005). In our study neither taxonomic groups (rotifers, calanoids and cyclopoids) nor species

(*Daphnia* spp., *Bosmina* spp.) showed significant differences in abundance related to disturbance indicating no change in bottom-up and top-down effects due to forest harvesting activities.

At the zooplankton community level, none of the studies including ours on short-term and mid-term impacts of logging on lentic ecosystems detected an ecological response to forest activities in species assemblages, suggesting that potential buffering processes in the littoral zone prevent changes at medium trophic levels to environmental perturbation (Rask *et al.* 1998, Patoine *et al.* 2002a, 2002b, Jalal *et al.* 2005). However, subtle changes in cladoceran species composition following forest harvesting were observed at a ten-year scale and were related an increase of nutrient (Bredesen *et al.* 2002). There might be a delay in detecting changes in biotic factors such as abundance, biomass and species composition after harvesting. Changes may accumulate over longer time scales before the response to disturbance becomes visible at higher trophic levels due to higher complexity. Definitely the initial changes take place at the bottom of the food web with water quality being impacted first. On the other hand, buffer strips around the lakes and littoral zones might be able to protect the impacts of harvesting activity in the pelagic zones, at least on a short time scale and within the range of 40% and 65% of catchment area being harvested.

Our results suggested that CLAAG plus the buffer strips along stream and lakes as done in our study area have an impact on water quality but not on phytoplankton and zooplankton in the pelagic zone of lakes. Winter harvesting (two lakes out of four in our study) reduce soil compaction and scarification due to frozen soil and snow cover of the treated area as compared with summer harvesting (Berger *et al.* 2004), ultimately reducing erosion in spring during snowmelt. Rask *et al.* (1998) showed as well that winter clear cut (15%–33% of catchment area) had less impact on water quality than the additional scarification (early summer). Unfortunately, most of the studies on the impact of harvesting and wildfire on lakes and streams did not mention the time of year during which harvesting activities were conducted.

Natural variability

High variation of physico-chemical and biotic variables among lakes and years within treatments occurred and were not related to the perturbation. This underlines the complexity and difficulty to detect perturbation effects that are hidden-overwhelmed with natural variability. We reduced spatial effects by choosing logged and control lakes at a relatively small geographic scale. In our study, the power to detect perturbation may be reduced by the small sample size of four lakes per treatment (total $n = 8$) which may not be enough considering the high inter-lake variability. Nevertheless, our sampling design clearly showed that a before and after perturbation approach with similar replication of treatment and control lakes is necessary to improve interpretation of the results. Without pre-perturbation sampling, there might be a risk of misinterpretation when attributing differences between treatments wrongfully to the perturbation while it is related to differences already present before harvesting in the two types of lakes (Downes *et al.* 2002).

Conclusion

In summary, harvesting seemed to have little short-term effect on the water quality and plankton in the pelagic zone of oligotrophic lakes of the eastern Canadian Boreal Shield. The only change detected which was related to logging, the increased DOC and TP concentrations, did not result in a bottom-up effect. Phytoplankton biomass and community structure of higher trophic levels showed high natural variability that seemed to be more important among lakes and sampling dates in logged as well as in control lakes. Therefore natural variability seemed to be important to influence ecological patterns within lakes than the short-term impact of harvesting. These findings support the conclusions drawn by previous studies on Canadian Boreal Shield lakes (Pinel-Alloul *et al.* 1998, Patoine *et al.* 2000, 2002a, 2002b, Planas *et al.* 2000). We hypothesise that novel logging strategies such as careful logging around advanced growth in

combination with 20-m buffer strips fringing streams and lakes might be an efficient protection to mitigate short-term effects of additional allochthonous matter input in lake pelagic zones after forestry activities on watersheds.

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Appendix. List of zooplankton taxa found in cut and control (cont) lakes over the entire sampling period (July 2003, September 2003, July 2004 and September 2004).

Species	Lakes							
	Cut-1	Cut-2	Cut-3	Cut-4	Cont-1	Cont-2	Cont-3	Cont-4
Rotifera								
<i>Ascomorpha</i> sp.	+	+	+	+	+	+	+	+
<i>Asplanchna priodonta</i>	+	+	+	+	+		+	+
<i>Cephalodella</i> sp.	+	+						
<i>Collotheca</i> sp.	+	+	+	+	+	+	+	+
<i>Conochiloides dossuarius</i>	+	+		+	+	+		
<i>Conochilus unicornis</i>	+	+	+	+	+	+	+	+
<i>Filinia</i> sp.		+						
<i>Gastropus hytopus</i> and/or <i>minor</i>		+	+	+				
<i>Gastropus stylifer</i>	+	+	+		+	+		+
<i>Kellicottia bostoniensis</i>	+	+		+	+	+		+
<i>Kellicottia longispina</i>	+	+	+	+	+	+	+	+
<i>Keratella cochlearis</i>	+	+	+	+	+	+	+	+
<i>Keratella quadrata</i>						+		
<i>Keratella taurocephala</i>				+	+			
<i>Ploesoma</i> sp.	+	+	+	+	+	+		
<i>Polyarthra</i> sp.	+	+	+	+	+	+	+	+
<i>Synchaeta</i> sp.	+			+	+	+	+	+
<i>Testudinella</i> sp.				+				
<i>Trichocerca</i> sp.	+	+	+	+	+	+	+	+
<i>Tylotrocha monopus</i>				+		+		
Cladocera								
Bosminidae	+	+	+	+	+	+	+	+
<i>Daphnia dubia</i>	+		+	+		+	+	+
<i>Daphnia longiremis</i>	+	+	+	+	+	+	+	+
<i>Daphnia pulex</i> complex ¹	+	+	+	+		+	+	+
<i>Daphnia</i> sp.	+	+	+	+	+	+	+	+
<i>Diaphanosoma brachyurum</i>	+		+			+		
<i>Holopedium gibberum</i>	+	+	+	+	+	+	+	+
<i>Latona setifera</i>	+				+			
<i>Leptodora kindtii</i>							+	
<i>Polyphemus pediculus</i>		+						
<i>Sida crystallina</i>	+		+	+				
Copepoda								
<i>Acanthocyclops</i> sp.		+						
<i>Acanthocyclops vernalis</i>		+						
<i>Cyclops scutifer</i>	+	+	+	+	+	+	+	+
<i>Cyclops</i> sp.	+	+		+		+	+	+
<i>Mesocyclops edax</i>	+	+	+	+	+	+		
<i>Tropocyclops prasinus mexicanus</i>	+	+	+				+	
Diaptomidae	+	+	+	+	+	+	+	+
<i>Epischura lacustris</i>	+	+	+	+	+	+	+	+
<i>Leptodiaptomus minutus</i>	+	+	+	+	+	+		+
Total	30	30	25	29	24	27	21	22

¹ *Daphnia pulex* complex includes *D. pulex*, *D. middendorffiana*, *D. catawba* and *D. pulicaria*.