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Impacts of watershed disturbance on phytoplankton and periphyton communities

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Impacts of watershed disturbance on phytoplankton and periphyton communities

by

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ABSTRACT

This project contributes to the understanding of the consequences of natural disturbances on communities at the base of the food web of the boreal forest lakes and the influence exerted by human activities in altering natural disturbance. The deliverable of the study is a quantitative model that could be easily applied to sustainable forest harvesting; this investigation also provides evaluation tools for environmental monitoring. The study compares, attributes of primary production (algal biomass), biodiversity indicators (algal species richness and diversity), and alga's quality (edible and non edible algae), from 16 pristine lakes, undisturbed for more than 40 years (reference lakes), 9 naturally disturbed lakes (50% -100% drainage basin was severely burnt in 1995) and 13 human disturbed lakes (8.5%-73% of the drainage basin was logged, 9 lakes in 1995, and 4 lakes in 1997 and 1998). The 37 lakes are located in the Canadian Shield Boreal Forest (47°52'-48°59' N and 73°19'-76°34' W) and have been selected by the Land-Aquatic Quebec team in collaboration with some of the supporting Eastern Industries. Results from four years of sampling demonstrate that, since year-1 after disturbance, algal biomass has been significantly higher in lakes of perturbed ecosystems than in pristine reference lakes. When only perturbed lakes were considered, for a similar % of disturbance, biomass was significantly higher in lakes on naturally perturbed basins than in those on harvested basins. Littoral algal (periphyton) biomass responses to disturbance were more than one and a half in lakes on post-harvested basins to three times higher in lakes on post-fired basins than pelagic algal (phytoplankton) biomass per unit area. In disturbed lakes increases of biomass were in general associated with changes in species composition. Phytoplankton community was dominated by mixotrophic nanoflagellates in reference lakes and in lakes on post-harvested basins, and by photoautotrophic diatoms in lakes on post-fired basins. Diatoms were the dominant taxa in periphyton for all lakes independently of disturbance. Biodiversity only decreases in forest harvested lakes systems with more than 40% of disturbance and a high drainage ratios. Five years after disturbance algal communities have not returned to the natural equilibrium conditions. Changes observed in the disturbed lakes could be predicted from an empirical model, by incorporating the area of the drainage basin disturbed and the sum of the area of lakes in the watershed. These two parameters alone accounted for more than 70% of variation in primary producers responses to disturbance. This simple model indicates the appropriate boundaries for sustainable forest harvesting when considering algal production, algal quality and species richness conservation. The model will be incorporated to a more general model integrating land, aquatic and forest practices.

RÉSUMÉ

Ce projet contribue à la compréhension de l'impact des perturbations naturelles et anthropiques sur les communautés à la base de la chaîne alimentaire des lacs de la forêt boréale. Les résultats contribuent à l'élaboration d'un modèle quantitatif facilement applicable au développement durable des forêts. Cette recherche peut également fournir des outils de surveillance environnementale. Cette étude compare des caractéristiques de la production primaire (biomasse algale), des indicateurs de biodiversité (richesse et diversité des espèces algales) et la qualité des algues (comestible ou non) dans 16 lacs témoins, non perturbés depuis plus de 40 ans (lacs de référence), 9 lacs perturbés naturellement (50 à 100% du bassin versant sévèrement brûlé en 1995) et 13 lacs perturbés par les activités humaines (8,5 à 73% du bassin versant coupé, 9 lacs en 1995 et 4 lacs en 1997 et 1998). Les 37 lacs de la forêt boréale (47º52'-48º59' N et 73º19'-76º34' O) ont été sélectionnés en collaboration avec quelques industries supportant le projet. Les résultats des quatre années d'échantillonnage démontrent que dès l'année suivant les perturbations, la biomasse des algues est significativement plus élevée dans les lacs perturbés que dans les lacs de référence. Lorsque seul les lacs perturbés sont considérés, pour un % de perturbation similaire, la biomasse est significativement plus élevée dans les lacs dont les bassins versant ont subi des perturbations naturelles en comparaison avec les perturbations anthropiques. La réponse de la biomasse des algues littorales (périphyton) par rapport à celle des algues pélagiques (phytoplancton; par unité de surface), est une fois et demi plus élevée dans les lacs où le bassin versant a été coupé et 3 fois plus élevée dans les lacs où le bassin versant a brûlé. Dans les lacs perturbés, l'augmentation de la biomasse est associée avec des changements dans la composition des espèces. La communauté phytoplanctonique est dominée par les nanoflagellés mixotrophes dans les lacs de référence et suite aux coupes forestières, alors que les diatomées (autotrophes) dominent suite à un feu de forêt. Les diatomées dominent la communauté périphytique dans tous les lacs indépendamment du type de perturbation. La biodiversité augmente seulement dans les lacs de coupe avec plus de 40% de perturbation et un ratio de drainage élevé. Cinq ans après les perturbations les communautés algales ne sont pas retournées à leurs conditions d'équilibre. Les changements observés dans les lacs perturbés peuvent être prédit par des modèles empiriques, incorporant l'aire du bassin de drainage perturbé et la somme de l'aire de tous les lacs du bassin. Ces deux paramètres expliquent plus de 70% de la variation de la réponse des producteurs primaires aux perturbations. Ce modèle simple indique des frontières appropriées pour le développement durable des forêts lorsque l'on considère la production algale, leur qualité et le maintien de leur biodiversité. Ce modèle peut être incorporé dans un modèle plus général intégrant les milieux terrestres, aquatiques et les pratiques forestières.

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INTRODUCTION

Forest landscape is rejuvenated and shaped by natural disturbances. Natural disturbances in Canadian Boreal Forest are dominated by wildfires, although insect outbreaks and windstorms are also occurring in some areas. In the last decades increasing pressure to provide timber and other resources from the Boreal forest, has raised public concern over the potential impact of these exploitations in terrestrial and aquatic ecosystems. A framework for sustainable resources exploitation must consider, and must know, the ranges of variability in ecosystems within natural conditions in order to set boundaries for human intervention. In spite of Canada being a forest nation, few studies have documented the consequences of disturbances in the Canadian Boreal forest, and up to now, no study has considered the entire watershed, including the aquatic systems, in their research. Aquatic ecosystems and their fisheries are intimately tied to the dynamics of surrounding landscapes, including the disturbance regime.

Lakes occupy almost a third of the Canadian Shield Boreal eco-region, their water and fish are a traditional resource for First nations' communities, and lakes are also very important for recreational purposes. One of the common, but poorly quantified, consequences of drainage basin disturbances is the mobilization of nutrients, contaminants and organic matter from soils to surface waters. In coniferous forest, soil losses of base cations, nitrate (NO_3) and total phosphorus (TP) following wildfires have been reported (Wright 1976, Bayley et al. 1992), and similar effects are usually observed with harvesting (Nicholson et al.1982, Plamondon et al.1982). In lakes the first expected response to these enhanced fluxes of nutrients is an increase in productivity and a shift in species composition of free-floating and littoral algae. Increases in algal productivity could change the trophic status of lakes and algal community changes could have a cascading effect on the entire food web. These changes could effect fish communities, e.g., if changes in species composition are associated with the growth of non edible and/or toxic algae that would decrease food availability for fish. Alternatively, increases of algal productivity could also decrease the oxygen concentration in the hypolimnion of lakes, impairing fish survival.

Few studies have documented the consequences of forest disturbances on the chemistry and biology of surface waters, and the majority of these studies have only considered impacts of disturbances on stream hydrology and chemistry (Likens et al. 1970, Plamondon et al. 1982, Bayley et al. 1992) and a few have addressed biota responses (Holopainen and Huttuten 1992, Rask et al. 1998). Furthermore, the former studies were concerned with only one type of disturbance (clear cutting or wildfire) but none - until the present SFM-NCE program - have compared the consequences of human activities to natural disturbance effects.

The aim of this study was to partially fill this lack of data, in understanding how the size of natural disturbance modify lake communities at the base of the food web and how these changes compared with those associated to harvesting. More specifically, we analyzed changes in biomass and community structure of pelagic algae (phytoplankton) in lakes on drainage basins disturbed by wildfire and harvesting. The final aim was to produce a model that could give guidelines to managers to keep the lakes within the boundaries of temporal and spatial natural oscillations. This model would be integrated in the general model that will guide Federal-Provincial governments in the development of rules for forestry harvesting, and it can serve as a tool for forestry industry.

Because of increasing evidence that the littoral as a habitat is crucial for fish feeding in Canadian Shield lakes and because benthivorous fish were the most widely distributed species in the study lakes (Magnan and St-Onge 1999), as of 1996 (year-2 after disturbance) the study of the littoral productivity was also undertaken in a subset of lakes (Planas et al. 2000; Groulx 2000). Responses of the littoral algae (periphyton) were compared to responses of phytoplankton in each lake where both communities were sampled.

Our working hypotheses were that: 1) Wildfire and forest harvesting, by increasing nutrients and organic matter inputs, would impact water quality and aquatic communities in disturbed boreal lakes compared to reference lakes. 2) Variation in water quality and biota among the three sets of lake types (reference, burnt and harvested) should be more important that among-lakes (in a given set), and within-lakes variation.

Our hypotheses were based on the knowledge that undisturbed forest ecosystems have very strong negative feedbacks, and efficiently retain nutrients and other elements in soil or in the permanent structure of plants (e. g., branches). Because watershed disturbances increase runoff, modify height of the water table and soil temperature, the geochemical cycling of soil elements should accelerate. Consequently, more nutrients, dissolved organic carbon, and other chemical elements will be exported from soils to aquatic ecosystems. The remarkably consistent response of algae to the increase of nutrients is well known (Schindler 1977), however, we do not know how algae will respond to nutrient increases associated with huge amounts of dissolved organic carbon.

This study is part of the Eastern Land-Aquatic team project whose principal investigators are R. Carignan, P. Magnan, B. Pinel-Alloul and D. Planas. We sampled the same lakes and we shared the data (see e.g. Carignan et al 1999a, b, Magnan et St-Onge 1999, Pinel-Alloul and Patoine 1999).

Part of this project research has already been published (Planas 1999, Planas et al. 1999, Groulx 2000, Planas et al. 2000). In this report, we will briefly summarize the main findings of the project and we will present new data (not yet published) on changes in community structure related to the type of disturbance.

METHODS

Study Area

The study area was centered on Gouin Reservoir (47º52'-48º59'N and 73º19'-76º43'W), at the transition zone between the boreal mixed and the boreal conifer forest (see, Carignan et al. 1999 a,b, 2000, Planas 1999, Planas et al. 1999, 2000, Lamontagne et al. 2000). In this region, where extensive forest harvesting operated, three severe wildfires occurred in summer 1995 (30 000 to 50 000 ha) that provided us the opportunity to simultaneously compare nearby lakes which have been disturbed either by wildfire or logging, and these which had remained undisturbed.

Thirty-eight lakes were selected on the basis of comparable morphometry, size and depth and with less than 20 % wetland (bog, fens, swamp) in the watershed (Carignan et al. 1999, 2000). Sixteen lakes were located in undisturbed drainage basins, untouched by fire or any anthropogenic influences for at least the last 40 years, but generally for more than 70 years(“Reference lakes” = RL). Nine lakes, of which 50-100% of their drainage basin area, have been severely burnt in 1995 (“Burnt lakes” = BL). Nine lakes have, between ≈ 11 and 96% of the drainage basin area, been logged in 1995, one in 1995 and 1997, and four in 1997 or 1998 (“ Harvested lakes” = HL). For lake locations see figure 1 in a previous report (Planas 1999).

Sampling

Phytoplankton was sampled three times per year, in spring (within two weeks of ice out), summer and fall from 1996 to 1999. Duplicate integrated samples of the euphotic zone (depth of 1% light penetration, between 2 and 5 m) were taken near the deepest part of the lake, concomitantly with the water chemistry, physical properties and zooplankton (Carignan et al. 1999, Garcia and Carignan 1999, Pinel-Alloul and Patoine 1999, Carignan et al. 2000, Patoine et al. 2000).

For periphyton, some subsets of lakes were considered. Five (5) RL in 1997 and 6 in 1998 and 1999, 5 lakes in fire-drainage basins, and 4 lakes on drainage basins harvested in 1997 and 6 in 1998 and 1999, were studied using artificial substrates (70 µm Teflon mesh; Planas 1999) placed to 1 m depth. Substrata were left in the field for either 3 months (summer benthic algae) or 9 months (winter benthic algae) or 12 months (Planas et al. 2000, Groulx 2000).

Phytoplankton and Benthic Algal Biomass Measurements

Chlorophyll-*a* (Chla) concentrations, and specific algal biovolumes were used as a measure of algal biomass for phytoplankton and benthic communities. Procedures on samples conservation, Chla extraction and biovolume measurements are detailed elsewhere (Planas 1999, Groulx 2000). Biodiversity was calculated as the mean of annual-total species richness per lake (Planas 1999, Groulx 2000).

Data Analysis

In order to compare the relative importance of pelagic and benthic algae, and to calculate the benthic algal biomass as percentage (%) of total biomass in each set of lakes, phytoplankton biomass per unit volume was transformed to unit area of photic zone ($mg.m^{-3}$ * photic zone depth in metres). Briefly, the benthic to phytoplankton biomass were estimated, respectively, from the average benthic biomass per lake times the littoral area, and the average phytoplankton biomass per lake times the area of the pelagic photic zone (see Planas et al. 2000 for more details).

Statistical analyses were performed on $\log_{10}$ transformed data when necessary, using SAS 6.14 or JMP packages (SAS Institute Inc). One-way or two-way ANOVA (general linear model, GLM) was used, respectively, for winter periphyton, and summer periphyton and phytoplankton data. Multiple regressions analyses were performed with a stepwise variable selection ($p < 0.05$ as an entering and keeping level). Normality of the predicted-observed residuals was verified with a Shapiro-Wilk W-test. Correlations between variables were calculated using the Pearson's product moment pairwise method (Legendre and Legendre 1998) (see Planas et al. 2000 for more details).

SUMMARY OF DATA ANALYSIS

Response of Algal Biomass

Since year-1 after disturbance pelagic mean Chla concentrations were significantly higher in lakes with more that 40% of the drainage basin disturbed (Planas et al. 2000). Among treatments, and for any given year, mean pelagic Chla had higher concentrations in BL, intermediate in HL and the lowest in RL (Planas et al. 2000). The temporal phytoplankton Chla response ratio (the ratio of mean Chla outcome for BL basins and HL to that in the RL; Hedges et al. 1999) differed through out the season and between years (Figure 1). Lakes on fire-drainage basins showed a higher response in 1997 and 1998 than in 1996, but the opposite was observed in HL where the lowest response ratio was observed in 1997. Within years and throughout the season, Chla concentrations tended to be higher in spring. Overall, for any set of lakes, higher Chla responses was measured in lakes with a drainage ratio (DR = area of drainage basin over the area of lake surface) higher than >4.

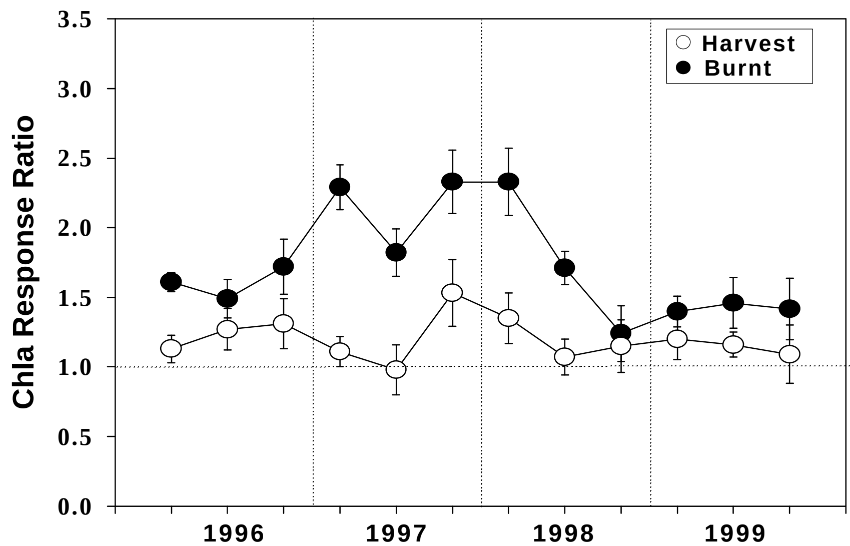

Figure 1 - Evolution of the monthly average pelagic algae relative Chla response ratio (1996 to 1999) of lakes located in perturbed watersheds as compared to reference lakes (dotted line). Burnt lakes (n = 9) and harvested lakes (n = 7)

In the littoral zone, periphyton biomass responses followed the same pattern than phytoplankton but responses were magnified (Figure 2). As observed for phytoplankton, for a given set of lakes differences between years are not related to number of years after disturbance. In BL, periphyton concentration was higher in summer 1997 (year-2) and lower in summer 1998 (year-3) (Groulx 2000, Planas et al. 2000). In an annual basis mean Chla concentrations in the littoral zone tended to be higher in winter (year-4) than in summer for any treatment (Figure 2). Among perturbed lakes, and at any season, BL had significant higher Chla concentration than HL (Planas et al. 2000, Figure 2).

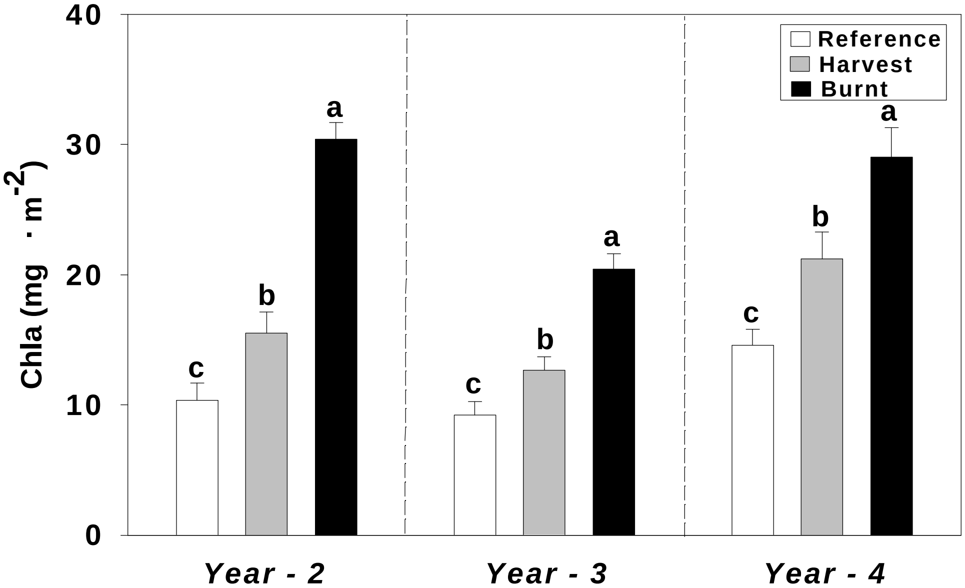

Figure 2 - Summer, (year-2 and year-3) and winter (year-4) means (± standard error) of periphyton chlorophyl *a* concentrations. Different letters indicate differences between set of lakes ($p \leq 0.05$).

In summary, in both communities, phytoplankton and periphyton, algal biomass was greater in lakes located within disturbed drainage basin. When both types of disturbances are compared, BL had a higher biomass than HL. Four years after disturbance, algal biomass may still not have reached a steady-state (Figure 3).

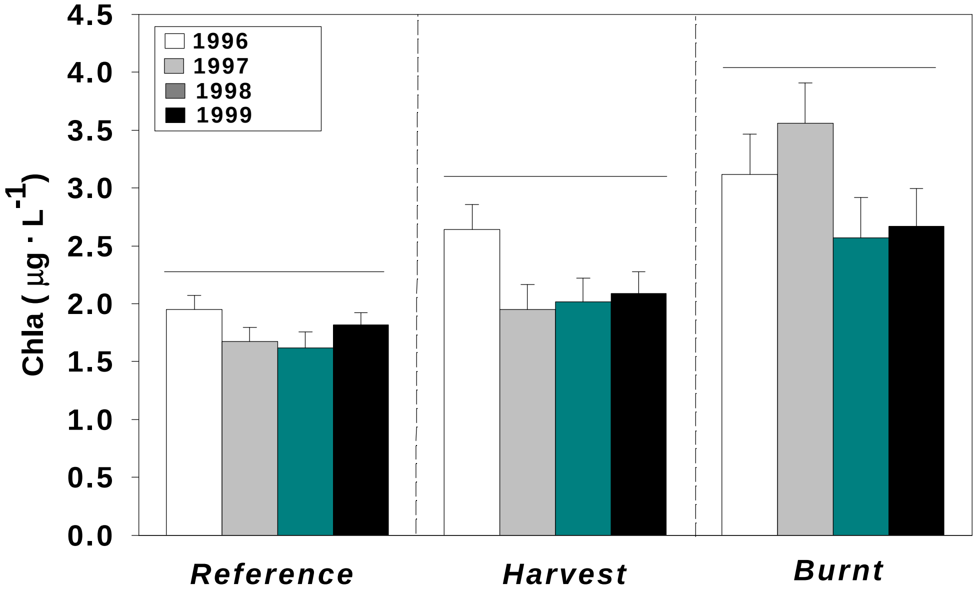

Figure 3. Evolution of mean (± standard error) of phytoplankton chlorophyl concentrations, in each set of lakes, from year-1 to year-4 after disturbance. Horizontal lines over bars, indicate not significant differences ($p \geq 0.05$) between years for any set of lakes.

Biomass Budget Between Phytoplankton and Periphyton

In the subset of seventeen lakes for which periphyton was sampled, we compared littoral versus pelagic Chla per unit area of photic zone. Chlorophyll-α was higher in periphyton than in phytoplankton (Planas et al. 2000). Differences between periphyton and phytoplankton Chla concentrations per unit surface were 200% HL and 300% in BL, no differences in Chla concentration were found between the two communities in RL.

In humic oligotrophic lakes, phytoplankton and benthic algae compete for nutrients (Hansson 1990). Nutrient loading in the littoral zone is less diluted than in the pelagic water column, and the efficiency of nutrient utilization, retention and recycling is much greater among closely aggregated littoral algal-microbial communities than in the pelagic zone (Wetzel 1996). These littoral characteristics lead to maximal resource utilization and productivity per areal unit. In lakes on disturbed drainage basins, in which benthic algal biomass was measured, nutrients in the water column were relatively abundant as compared to unperturbed lakes, suggesting that competition for nutrients between littoral and pelagic zones was weaker in relation to RL. For the BL in which benthic algae were studied, the 1997 and 1998 mean euphotic zone to mixing depth ratio (Z_{ph}/Z_{mix}) was lower than 1 ($Z_{ph}/Z_{mix} = 0.796 \pm 0.106$) and less than in the RL ($Z_{ph}/Z_{mix} = 1.31 \pm 0.101$) while the ratio in HL was intermediate and close to 1 ($Z_{ph}/Z_{mix} = 0.992 \pm 0.106$).

In summary, the periphyton algae showed a greater response to disturbance than phytoplankton algae. Responses are somewhat different for BL as compared with HL basins. The higher responses of periphyton communities as compare to phytoplankton in disturbed lakes could be explained by lower light penetration in the water column than in RL. Consequently, the ratio Z_{ph}/Z_{mix} decreases, diminishing time that phytoplankton is exposed to light during day hours.

Environmental Factors Influencing Algal Biomass

Phytoplankton Chla responses could be predicted either from watershed characteristics, or by physical and chemical lake characteristics.

Watershed characteristics influencing algal biomass

Multiple regression analysis between pelagic algae Chla concentrations, and watershed and lake parameters, showed that around 55% of the variance was explained by, the fraction of the catchment perturbed (F, Carignan et al. 1999), the 1/water residence time (T) or the drainage ratio (AD/AL = drainage area to lake area), and the percentage of the slope (Table 1, a and b). In equation b, 1/mean depth (Z_{mean}) also entered in the equation but it only explains 3% of the variance. The equivalent predictive power of T and AD/AL could be expected since we know that for a region, with similar annual precipitation, drainage basin area are related to water residence time, and that in boreal lakes many average properties can be reliably predicted from the ratio AD/AL (Schindler 1971; Fee 1979, Carignan et al 1999; Planas et al. 1999). In our studied lakes a strong correlation was found between T and DA/LA (r= -0.7931).

Table 1 : Multiple regression model between phytoplankton chlorophyll-a (dependent variable) and watershed and lake characteristics[1] (independent variables).

Model	$p_1 > \| t \|$	SE	r^2	adj r^2	*Prob > F*
a) With water residence time					
log (CHA)		0.077*	0.564	0.553	<0.0001
0.353	<0.0001	0.024			
0.002 F	<0.0001	0.002	0.346		
0.012% slope	<0.0001	0.002	0.113		
-0.034T(Year)	<0.0001	0.007	0.105		
b) With DA/LA					
log (CHA)		0.077*	0.558	0.542	<0.0001
0.378	<0.0001	0.47			
0.002F	<0.0001	0.0002	0.276		
0.008DA/LA	0	0.002	0.159		
0.012% slope	<0.0001	0.002	0.094		
$-0.176\log_{10}(Z_{mean})$	0.008	0.065	0.03		

[1]Watershed and morphometric data (Carignan laboratory). F = fraction of catchment perturbed (Carignan et al. 1999); DA/LA = Drainage area/Lake area; T = water residence time (year); %slope = % watershed slope; Z_{mean} = mean depth of the lake.

Table 2: Multiple regression (for summer data) or simple regression (for winter data) between benthic algae chlorophyll-a concentrations (dependent variable) and watershed and morphometric and hydrological lake characteristics[1] (independent variables).

Model	$p_1 < \|t\|$	SE	r^2	adj r^2	*Prob > F*
a) Summer growth					
log (CHA)		0.129*	0.79	0.755	<0.0001
1.49	<0.0001	0.104			
0.501F	<0.0001	0.072	0.443		
-0.075°litslop	0.0007	0.018	0.334		
-1.5e-7Vepi	0.0005	0	0.047		
b) Winter growth					
log (CHA)		0.134*	0.73		<0.0001
1.619	<0.0001	0.069			
-0.304	<0.0001	0.048			
c) Winter growth					
log (CHA)		0.173*	0.553		0.0006
0.81	<0.0001	0.106			
0.069DA/LA	0.0006	0.016			

[1]Watershed and lake data (Carignan laboratory). F = fraction of the catchment perturbed (Carignan et al. 1999); °litslop = mean littoral slope in degres; Vepi = volume of the epilimnion (m^3); DA/LA = Drainage area/Lake area; T = water residence time (year).

When the same watershed and lake characteristics were applied to summer benthic algae Chla, 75 % of the variance was predicted by F, the 1/mean littoral slope (^{o}litslop) and the 1/ volume of the epilimnion (Vepi), the latest variable explaining only 5 % of the total variance (tableau 2 a). Because the lower number of observations for the winter-fall benthic algal Chla concentrations we could not apply multiple regression. Using simple regression, the strongest empirical relationship between fall-winter Chla concentration and watershed was found with 1/T. The water residence time explained 73 % of the total variance (table 2, b). The ratio DA/LA was also a good predictor of winter CHA concentrations, explaining around 55 % of the variance (Table 2, c).

Physical-chemical variables influencing algal CHA

Phytoplankton Chla responses in lakes could also be predicted from the physical-chemical variables. Total phosphorus (TP) explained 48% of the partial variance, followed by the light extinction coefficient (ϵ_{PAR}) and dissolved inorganic nitrogen (DIN = NO_3 +NO_2 +NH_4) which explained 6 % and 4 % of the variance, respectively (Planas et al. 2000).

TP was also the best predictor of summer periphyton Chla concentrations, explaining 67 % of the variance, followed by nitrate (NO_3) and dissolved organic carbon (DOC) which accounted for 13 and 5 % of variance, respectively (Planas et al. 2000). Total phosphorus also showed a relationship with winter benthic algae Chla (r^2 = 0.622), but total nitrogen (TN) and DOC explained a stronger % of the variance (r^2 = 0.681 and r^2 = 0.606, respectively) (Planas et al. 2000)

In summary, % of disturbance, catchment characteristics and water residence times are good predictors of algal responses in Canadian Shield lakes. Prediction are somewhat improved when water quality variables such as nutrients or light penetration are used instead of morphometric or hydrological characteristics. Phosphorus is the main nutrient controlling the growth of the algae. But, the response of the algae to nutrient in mitigated by the decrease in light penetration, particularly in HL.

Pelagic Algal Community Structure

Changes in species composition

Community changes in species composition occur in disturbed lakes, particularly in phytoplankton communities. Non-toxic Cyanobacteria, the most abundant taxa within the picoplankton fraction of RL, decreased in HL since year-1 after disturbance, and continues to diminishes through the whole study period. All taxa, except Cyanobacteria, increased in BL with a large DR. However, the more drastic changes in community composition in BL was the increase of diatoms, which biomass increases almost one order of magnitude in relation to RL and HL. Harvesting barely changed the phytoplankton community composition in relation to RL, but the relative proportion of the different taxa was modified. As already mentioned, non-toxic Cyanobacteria decrease, phytoflagellates augmented, particularly Chrysophyceae, and to lesser extent Cryptophyta and Dinoflagellates (Planas 1999; Planas et al. 2000). These phytoflallegates have several species that are mixotrophic, this means that they have two modes of nutrition, autrotophic, using light to synthesize inorganic carbon and heterotrophic using particulate and/or dissolved organic compound for growth. The mixotrophic algae used the heterotrophic mode of nutrition when light, and/or nutrients, becomes limiting (see review Isaksson 1998).

The watershed disturbance changed the proportion of mixotroph algae in relation to autotroph. The ratio between mixotrophic algae and autotrophic algae was .significantly different (Oneway Anova, *Prop> F* <0.0001) between the sets of lakes. Lakes on harvested -drainage basin had the highest ratio and BL the lowest, RL having an intermediate ratio (Figure 4) These differences were mainly driven by the development of autotrophic diatoms in BL and mixotrophic chrysophytes in HL. In BL, autotrophic biomass was significantly higher than in HL and RL (Figure 5).

Autotrophic algae were the more important taxa in the periphyton communities of all lakes. Periphyton communities were dominated by diatoms in all lakes and no significant differences were found in taxa biomass between lake sets (Groulx 2000).

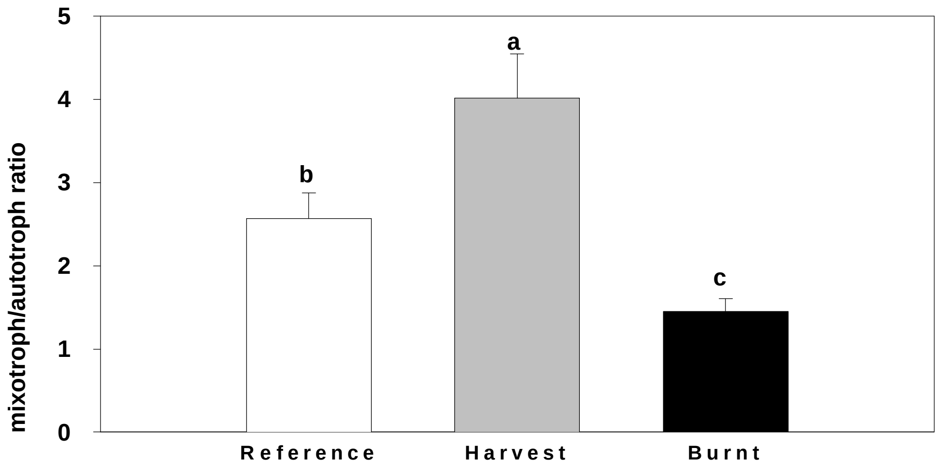

Figure 4 - Comparison means (± standard error) of mixotroph over autotroph ratio for phytoplankton, in reference and disturbed lakes. Different letter indicate differences ($p \leq 0.05$) between set of lakes.

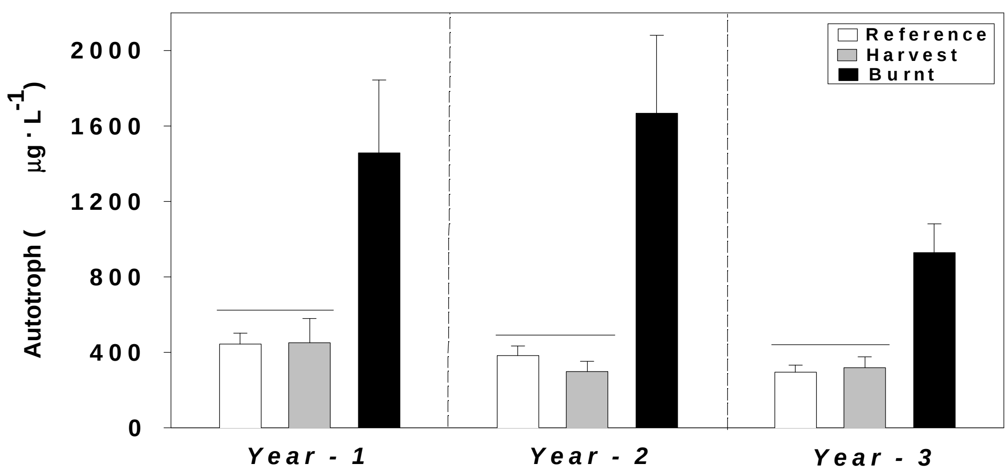

Figure 5 - Annual mean (± standard error) of autotroph phytoplankton biomass in each set of lakes in year-1, year-2, and year-3 after disturbance. Horizontal lines above bars indicate not significant difference (($p \geq 0.05$) between set of lakes.

The same physical and chemical variables that explained the biomass concentrations, explained the abundance of different taxa (light extinction coefficient, phosphorus and to a lesser extend nitrogen) (Planas 1999; Planas et al. 2000). However, the relative importance of each variable was different by considering only autotrophic taxa (Table 3). For autotrophic algae, the best predictor of biomass was DIN, (34% of the total variance), followed by the light extinction coefficient (15% of the total variance), and finally TP only explain 7% of the variance.

Table 3 : Multiple regression model between autotroph biomass (dependent variable) and watershed and lake characteristics[1] (independent variables).

Model	$p_1 > \| t \|$	SE	r^2	adj r^2	*Prob > F*
a) With water residence time					
log (autotroph)		0.230*	0.562	0.548	<0.0001
1.142	<0.0001	0.167			
0.441logDIN	<0.0001	0.067	0.338		
-0.313 ε_{PAR}	<0.0001	0.055	0.151		
1.423logTP	<0.0001	0.007	0.073		

[1]Watershed and morphometric data (Carignan laboratory). DIN = Dissolved inorganic nitrogen; ε_{PAR} = light extinction coefficient; TP = total phosphorus.

In summary, disturbance modifies the community composition, the changes went in opposite direction in both types of disturbance, mixotrophic algae increased in HL and autotrophic algae increased in BL. Mixotrophic algae were also abundant in RL, but the ratio of mixotrophic over autotrophic was higher in HL. Non toxic algae have developed in lakes located on disturbed-drainage basin, but some of mixotrophic algae species present in the study lakes (e. g., *Chrysosphaerella longispina*) have long spines and would not be ingested by herbivorous. Whereas proliferations of autotrophic taxa, and particularly diatoms increased the nutritious quality of food for herbivorous (Serge Paquet, Dolors Planas, unpublished).

Biodiversity

The mean number of species found in a given year was around 75 in RL. Half of the total number of species present in the study lakes pertain to the Chrysophyceae group. Green algae, although with low biomass in our study lakes, were highly diversified, too. No significant decrease on species biodiversity was measured in BL, although non-toxic Cyanobacteria numbers tends to be lower than in RL. However, a decrease in biodiversity was observed in HL with a high DR Lower biodiversity in HL became significant in year-3 after disturbance (Planas 2000). The decline in biodiversity in HL was due to the diminution in the number of Cyanobacteria species (Figure 6). Chrysophyceae biodiversity was higher in BL than in reference lakes as well as Dinoflagellates (Figure 6)

A negative relationship was found between total biodiversity and light extinction coefficient in our lakes, suggesting that light could be the variable that impairs growth of some algae. Pearson correlation coefficient between physiscal-chemical variables and algal taxa biodiversity demonstrate a negative correlation between Cyanobacteria and light extinction coefficient ($r = -0.5193$, $p = 0.0001$). In our lakes, underwater spectral irradiance was controlled by DOC, and a strong correlation was found between this variable and light extinction coefficient (Carignan et al. 2000). Harvested drainage areas exported more DOC (2 to 3 fold reference; Lamontagne et al. 2000) than natural disturbed drainage basins. In 1997, DOC runoff increases, 50 - 80 %, on harvested basins (S. Lamontagne, personal communication. GRIL-U. Montreal, C.P. 6128, Montreal, H3C 3J7), compared to the year before and the following years in the region of the Gouin Reservoir (Lamontagne et al.2000). Higher DOC concentrations in 1997 could explain the delayed decrease on algal biodiversity in HL.

Periphyton algal biodiversity in HL was not significantly different than in lakes on undisturbed drainage basins. However, periphyton algal biodiversity was significantly lower in BL (Groulx 2000).

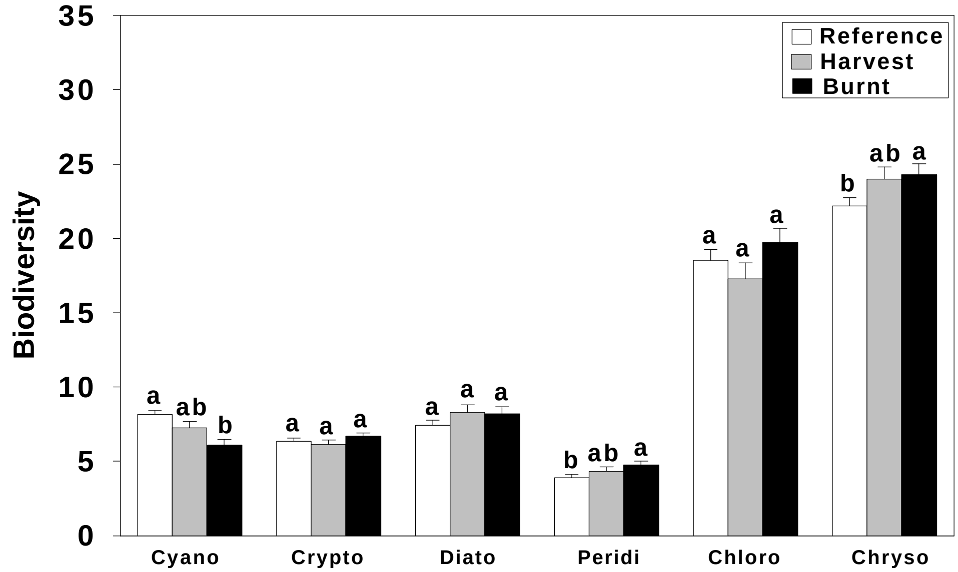

Figure 6 - Three years mean (± standard error) of biodiversity in different phytoplankton taxa. For a given taxa, different letters above bars indicate significant difference between set of lakes ($p \leq 0.05$). Cyano = Cyanobacteria, Crypto = Cryptophyta, Diato = Diatoms; Peridi = Dinoflagellates, Chloro = Green algae, Chryso = Chrysophyceae.

In summary, in phytoplankton communities, algal diversity in BL was not distinguishable from lakes in undisturbed drainage basin. However, in HL, algal biodiversity decreased where the disturbance was relatively large. This decline on biodiversity was probably due to a reduction in light penetration.

MANAGEMENT APPLICATION

During the 5 years of study, algal productivity in lakes located in post-fire and in post-harvesting drainage basins was significantly higher than in lakes of undisturbed drainage basin. Phosphorus, and to lesser extent nitrogen, seems to be responsible of algal productivity increases. Changes in biomass were higher in lakes located on post-fire drainage basins than in lakes located in post-harvested drainage basins. These differences could be explained by the light extinction coefficient. Light penetration was lower in lakes on harvested-drainage basins than in lakes on fire-drainage basins. In the study lakes, light penetration is strongly related to dissolved organic matter concentration (Carignan et al. 1999a,b, 2000), as it has been observed in other Canadian Shield lakes. Thus, lower algal response in post-harvested lakes than in post-fire lakes are associated with differences in the amount of allochthonous dissolved organic matter, which is higher in drainage basin impacted by logging than in naturally disturbed drainage basins (Lamontagne et al. 1999, 2000). Lower light penetration in lakes located on post-harvested drainage basins is also responsible for differences in algal community attributes (changes in biodiversity and/or species composition). For a given set of disturbed lakes (naturally disturbed and human disturbed) the variance in the responses were very high when all lakes are pooled together (see figure 1).

Although we could not account for the influence of natural inter-annual variability due to the lack of pre-disturbance data our study does, however, indicate that this variance diminishes considerably when the drainage ratio (DR = drainage area over lake are) and the percentage of disturbance are considered. Responses in disturbed lakes with low drainage ratio and/or less than 30% of disturbance in the drainage basin were not significantly different that in reference lakes. However, responses in lakes on high drainage ratios and high levels of percentage disturbance were consistently higher than in reference lakes.

This finding allows us to built simple empirical models incorporating disturbance scenarios and variables, such as lake area, which can be easily measured from maps. More precisely, the relationship between the area of the perturbed drainage basin and the summation of the lakes' area in the watershed (FA = WAP/ΣLA) we are able to predict more than 70 % of the variance in algal biomass on disturbed lakes (Planas et al. 2000; Figure7) and/or algal attributes (Planas 2000). This relationship also allows to predict variables of lake water quality, such as dissolved organic carbon or phosphorus (Carignan et al. 2000).

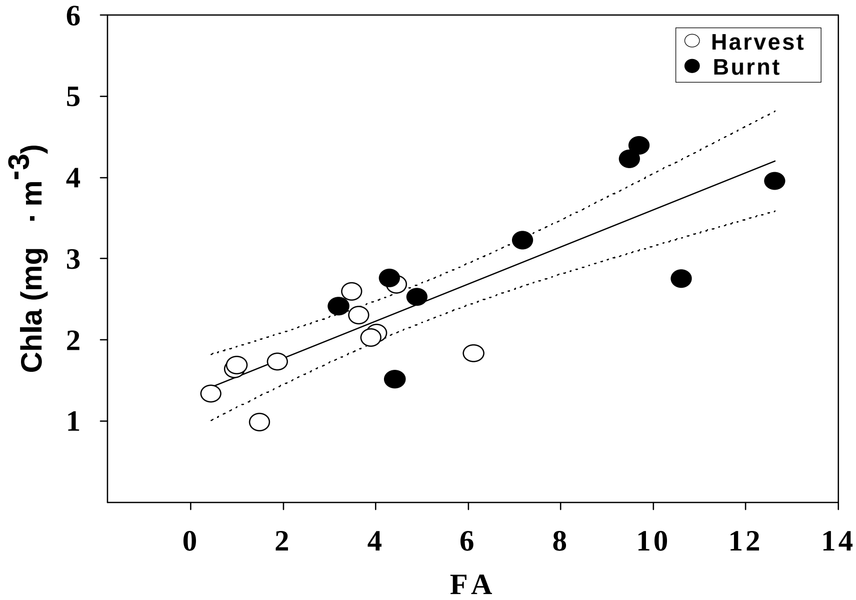

Figure 7 - Relationship (solid line) and 95 % confidence intervals (dotted lines) between phytoplankton chlorophyll α (y-axis) in perturbed lakes and the fraction of the watershed disturbed over the ∑ lakes surface area in the watershed (FA; x-axis) (From Planas et al. 2000).

The proposed empirical model is a simple tool that uses a small number of independent parameters. These parameters are easily available from maps describing catchment and lakes areas. This model can also be integrated to a more general model integrating Land, Aquatic and Forest Practices.

To consider the size of drainage basin and lake areas in harvesting planning is imperative for the maintenance of the desirable trophic status of lakes. Lakes in perturbed drainage basins with large DR have reached the oligo-mesotrophic status. Still we do not know (we lack of longer term data to certify it) if the disturbed lakes have overpassed the resilience mechanisms that will lead the aquatic ecosystems to return to natural conditions. If human drainage basin disturbances had been as important as the 1995 fires our conclusion would probably be completely different and more pessimistic. Our forecast in such conditions is that the export of organic matter from the harvested drainage basin could affect fish communities in such pristine boreal lakes.

For future environmental monitoring, on the responses of lake biota to disturbance, we recommend to follow the evolution of periphyton communities. The reason for this recommendation are: i) periphyton communities are at the base of the littoral food web and littoral is an important habitat for fish feeding; ii) periphyton responses to disturbance are probably faster, and greater, than phytoplankton; iii) sampling could be easily done using the artificial device that we developed together with Richard Carignan (see Planas 1999, Figure 2, p. 5); and iv) one sampling per year would be enough since the device can stay in the lake for 1 year, and new devices could be installed at the same time as the retrieval of those that have been colonized the former year.

The former recommendation should allow planners to maintain healthy aquatic ecosystems, while providing economic, social, and cultural opportunities for the benefit of present and future generations.

CONCLUSIONS

Phytoplankton biomass as well as the dominant taxa in RL of our study region were characteristic of pristine oligotrophic Canadian Shield lakes. Within disturbed lakes, volumetric phytoplankton biomass increased to mesotrophic levels (Chla > 3 mg•m^{-3}, biomass > 3000 mg•m^{-3} w.w.) with maximum Chla concentrations greater than 5 mg•m^{-3} in BL. Different responses in relation to the type of disturbance were found at the algal community level. Increases in taxa such as the edible diatoms, that are characteristic of enriched boreal lakes, only occurred in BL. In HL biomass augmentations was associated to the increase of mixotrophic algae. Periphyton biomass responses to drainage basin disturbances followed the same pattern as for phytoplankton; the response was, however, magnified relative to the pelagic community. In BL benthic algal Chla as high as 100 mg•m^{-2} was measured two years after disturbance, while in references lakes, the highest Chla concentration measured was approximately 30 mg•m^{-2}.

Even four years after disturbance algal communities in lakes have not reached a steady state; long term responses to disturbances have been reported in aquatic ecosystems following wildfires (Minshall et al. 1997). During our 4-year study, the greatest response was measured in year-2 following disturbances and the sign of the response was different in relation to the type of disturbance. Biomass increased and major taxa shifts were observed in BL, whereas biomass decreased in HL.

These inter-annual differences between disturbances could be explained by the variability in chemical fluxes and light penetration related to runoff and the type of disturbance. With similar nutrient loadings, low light transmission could explain, for any year and throughout the seasons, the small response of algal biomass in HL as compared to BL. Low light, when nutrients are available, could limit algal primary production and hence biomass. For a similar increase of nutrients in perturbed lakes, differences in the ϵ_{PAR} could also explain different responses in the algal taxa responses.

The littoral versus pelagic biomass (Chla) per unit of surface area indicated a stronger response of littoral communities to disturbances. These littoral responses could lead to maximal resource utilization and positively influence the fish productivity. This is a new finding, no other studies investigating the impact of drainage basin disturbance on lakes have simultaneously measured the response of pelagic and benthic algae, however, further research is needed in order to obtain a better understanding.

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