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Impact of forest harvesting on larval and juvenile growth of yellow perch (*Perca flavescens*) in boreal lakes

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Any factor modifying early growth in fishes could lead to large recruitment variations. We investigated the impact of forest harvesting on growth rate and length-at-age of larval and juvenile yellow perch (*Perca flavescens*) and on the trophodynamics in small oligotrophic Canadian Boreal Shield lakes. Yellow perch, phytoplankton, and zooplankton were sampled in August or early September in three consecutive years (2003, 2004 and 2005) from three unperturbed lakes and from three lakes that had had logging in their watershed catchment zones after the first year of sampling. Two years after the perturbation, larval and juvenile growth rate and length-at-age of yellow perch, as well as Chl *a*, were significantly higher in lakes perturbed by forest harvesting than in unperturbed ones. Our results support the hypothesis that early growth of yellow perch has been favoured in perturbed lakes. This may have been due to post-harvest enhancements in nutrients and dissolved organic carbon concentrations, likely generating bottom-up changes in larval and juvenile yellow perch feeding conditions such as increased prey abundance and visibility thus, stimulating growth.

Introduction

A considerable body of evidence suggests that high mortality of fishes during their early life stages is not random (Houde 2002). The leading hypotheses concerning recruitment rather propose that mortality is size- or growth-selective. According to the "growth-mortality" hypothesis (Anderson 1988), fast-growing individuals have a higher probability of survival considering that (1) they are less vulnerable to predation than smaller conspecifics at a given age (the "bigger-is-better" concept; Miller *et al*. 1988), (2) they spend less time in the highly vulnerable larval stage (the "stage-duration" concept; Chambers and Leggett 1987, Houde 1987), and (3) they are more likely to escape from predators at a given size (the "growth-selective predation" concept; Takasuka *et al*. 2003). Given the critical importance of growth during the early life stages, factors influencing growth rate could lead to significant fluctuations in survival and recruitment.

The environmental conditions experienced by fishes may vary from one freshwater system to another, and these variations could have a strong influence on larval growth (Claramunt and Wahl 2000). Environmental conditions may also change following a perturbation and could generate variations in fish feeding, growth, and survival. Forest harvesting in catchments is a major perturbation for northern Canadian Boreal Shield lakes. Several studies have documented the impact of forest harvesting on water quality and trophodynamics in Boreal Shield lakes (*see* Pinel-Alloul *et al.* 2002b). In general, forest harvesting in lake watersheds increases the concentration of nutrients such as total phosphorus (P_{tot}) and total nitrogen (N_{tot}), as well as dissolved organic carbon (DOC) in the water (Rask *et al.* 1998, Carignan *et al.* 2000, France *et al.* 2000, Steedman 2000, O'Driscoll *et al.* 2006, Winkler *et al.* 2009). Bottom-up forces may act at the primary-producer level, as revealed by the slight enhancement of pelagic and periphytic Chl-*a* concentrations noted in several studies (Planas *et al.* 2000, Steedman 2000, Nicholls *et al.* 2003, Ghadouani *et al.* 2006). However, effects on primary producers could be smaller than expected considering the increased nutrient input because of light attenuation caused by higher DOC concentrations (Pinel-Alloul *et al.* 2002a). Studies on impact of forest harvesting on zooplankton had shown conflicting results: some reported no impact on abundance, diversity, size spectra, or species assemblages (Patoine *et al.* 2002a, 2002b, Winkler *et al.* 2009), while others revealed a decrease in calanoid copepod biomass (Patoine *et al.* 2000), an increase in crustacean abundance (Rask *et al.* 1998), or an increase in the biomass of zooplankton < 500 μm in size (Bertolo and Magnan 2007). These inconsistencies in the reported effects of forest harvesting on zooplankton could be due to top-down forces driven by zooplanktivorous organisms or an enhanced complexity of interactions with higher levels of the trophic web (Northcote and Hartman 2004).

Results concerning the impact of forest harvesting on fish are also variable. Almost all studies have focused on adult fishes. However, early life stages are more likely than adults to be affected by trophic perturbations given the attenuation of bottom-up forces with higher trophic levels (McQueen *et al.* 1986, DeMelo *et al.* 1992). Only two field studies have documented the impact of forest harvesting on early life stages of fish. St-Onge and Magnan (2000) reported a decrease in the abundance of small size classes of yellow perch (*Perca flavescens*) and white sucker (*Catostomus commersonii*) in eastern Canadian Boreal Shield lakes. However, their methods were not intended to catch young-of-the-year (YOY) fish, possibly inducing bias in the results (Bertolo and Magnan 2007). Using gear appropriate for sampling young fish, Bertolo and Magnan (2007) showed an increase in YOY yellow perch abundance after forest harvesting in lake catchments.

Yellow perch is a common forage fish in Boreal Shield lakes, and early life stages are easy to capture in their pelagic and littoral phases (Cucin and Faber 1985, Whiteside *et al.* 1985). Yellow perch is an open-substrate spawner and completes its entire life cycle within the lake, so it is not affected by spawning ground siltation that typically results from forest harvesting (Hartman and McMahon 2004). Yellow perch larvae and early juveniles are zooplanktivorous (Mills and Forney 1981, Whiteside *et al.* 1985, Post and McQueen 1988, Graeb *et al.* 2004) and could be affected by a change in their prey field due to bottom-up effects related to logging in the watershed.

The principal objective of this study was to measure the impact of forest harvesting on the growth rate and length-at-age of larval and juvenile yellow perch in small oligotrophic Boreal Shield lakes. We also tried to determine if variations in growth rate and length-at-age were related to Chl *a* and zooplankton biomass. We hypothesized that early life stages of yellow perch in perturbed lakes may take advantage of a slight increase in productivity due to forest harvesting, resulting in their higher growth rates as compared with fish in unperturbed lakes.

Material and methods

Study sites and sampling design

The lakes examined in this study are located in the Canadian Boreal Shield ecoregion in the province of Quebec, near Lake Mistassini (50°17´–50°41´N, 73°15´–72°49´W) (Fig. 1 and

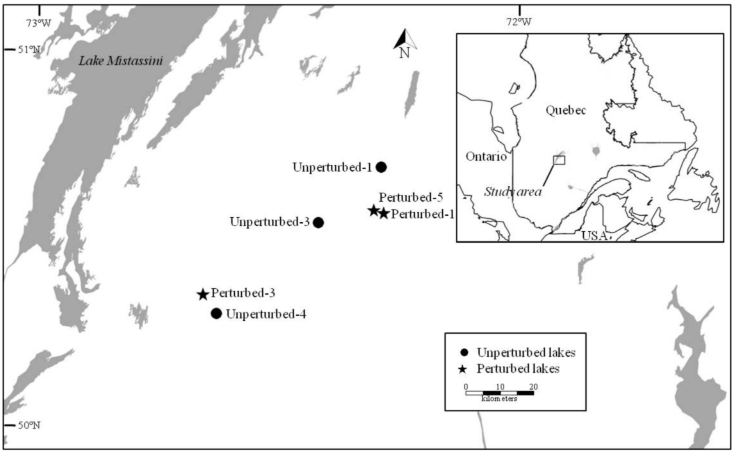

Fig. 1. Map of the study area showing the locations of perturbed and unperturbed lakes.

Table 1). Lakes in this area are typically oligotrophic and shelter fish communities mainly composed of northern pike (*Esox lucius*), walleye (*Sander vitreus*), white sucker, and yellow perch (Table 1). This region is characterized by spruce-moss landscapes exploited by the forest industry.

Six lakes were selected and assigned to one of the two lake treatments: perturbed or unperturbed lakes (Table 1). A multivariate procedure (ANOSIM procedure on euclidian distances matrix, PRIMER ver. 6 statistical package; Clarke and Warwick 2001) was used to compare lake characteristics between treatments before the perturbation. No significant difference was found between the two treatments for 12 variables measured at the onset of the study: shoreline development, catchment area, turnover rate, secchi depth, euphotic zone temperature and dissolved oxygen (DO), surface pH and conductivity, total phosphorus (P_{tot}), total nitrogen (N_{tot}), dissolved organic carbon (DOC), and chlorophyll *a* (Chl *a*) (Table 1, ANOSIM: $R = 0.48, p = 0.10$).

The sampling design included one survey before the perturbation (2003) and two surveys after forest harvesting (2004 and 2005). Forest harvesting occurred in autumn 2003 and/or winter 2004 (Table 1). Access to perturbed lakes in 2003 and unperturbed lakes was only possible by seaplane due to their pristine watersheds. Forest was cut using the careful logging around advanced growth strategy (CLAAG) and 20 m strips of standing forest was kept along lakes and streams after harvesting activities. An impact of forest harvesting on Boreal Shield lake water quality is more likely to occur when the drainage ratio of the lake (catchment area/lake area) exceeds 4 and when more than 30% of the catchment area is deforested (Carignan *et al*. 2000). Since all perturbed lakes had a drainage ratio > 5 and at least 33% of the catchment area was deforested (Table 1), we anticipated an impact on water quality.

Field sampling

Fish

YOY yellow perch were sampled from 12 to 28 August in 2003, 17 August to 1 September in 2004, and 1 to 4 August in 2005. YOY fish were captured with experimental monofilament gillnets 22.86 m long × 2 m deep that had three randomly placed panels with the mesh size of 9.5, 12.7, and 19.1 mm. Ten gillnets were randomly set perpendicular to the shore in each lake for one night on each sampling date. Due to the early sampling in 2005, we used an additional sampling method to target all size classes as suggested by Scharf *et al*. (2009): YOY fish were also caught with a beach seine (4 m long × 1 m deep, 500 μm mesh) at six sampling stations in each lake. All fish samples were preserved in 95% ethanol and transferred within 24 h in new 95% ethanol to avoid alcohol dilution and otolith damage (Butler 1992).

Plankton

Chl *a* was sampled on 2–9 September 2003, 8–9 September 2004, and 8 August 2005. Three independent, integrated water samples were taken at the deepest point of each lake in the euphotic zone, estimated as 1.25 times the Secchi depth for eastern Boreal Shield lakes (R. Carignan, Université de Montréal, pers. comm.).

Pelagic zooplankton was sampled during the same surveys as the Chl *a* except in 2005, when zooplankton was sampled during the fish survey (1–4 August 2005). Three vertical hauls were taken from 1 m off-bottom to the surface at the deepest point of each lake using a cantilevering zooplankton net (53 μm mesh) with a circular mouth opening of 0.25 m (Winkler *et al*. 2009). Zooplankton was anaesthetized with carbonated

Table 1. Limnological parameters of the six studied lakes in 2003, before the perturbations. x = presence of the fish species.

Lake parameters	Perturbed lakes			Unperturbed lakes		
	Pert.-1	Pert.-3	Pert.-5	Unpert.-1	Unpert.-3	Unpert.-4
Morphological parameters						
Altitude (m)	492	478	497	504	513	482
Latitude N	50°33´48´´	50°20´56´´	50°34´07´´	50°41´19´´	50°32´19´´	50°17´50´´
Longitude W	72°33´30´´	73°18´30´´	72°35´50´´	72°33´45´´	72°49´44´´	73°15´10´´
Maximum depth (m)	9.8	12.6	13.4	10.9	24.0	14.5
Lake area (km^2)	0.7	0.4	1.5	1.1	0.6	0.5
Lake perimeter (km)	7.7	5.1	8.6	5.6	6.2	4.4
Fetch (km)	2.1	1.6	2.9	2.2	1.5	1.7
Shoreline development (km)	2.6	2.0	2.0	1.5	2.3	1.7
Catchment area (km^2)	4.2	3.0	7.6	3.8	2.5	1.2
Catchment perimeter (km)	12.4	9.4	17.4	11.0	8.2	6.8
Catchment mean slope (%)	6.6	8.2	11.5	5.4	5.7	6.6
Drainage ratio	5.9	7.1	5.0	3.5	4.3	2.3
Order	1	2	2	1	1	1
Lake volume (× 10^3 m^3)	1835.2	1931.6	8315.7	4299.1	3990.3	2957.8
Turnover rate (N per year)	1.2	1.0	1.1	0.5	0.4	0.3
Harvested area (% of catchment area)	57.1	50.6	33.5	–	–	5.1
Time of harvest	Autumn 03	Winter 04	Autumn 03	–	–	–
Physicochemical parameters						
Secchi depth (m)[a]	1.5	1.5	2.1	2.0	3.0	3.8
Euphotic zone temperature (°C)[a]	12.8	12.2	13.4	12.9	11.9	12.7
Euphotic zone DO (mg l^{-1})[a]	11.0	7.5	10.6	11.1	7.7	7.8
Surface pH[a]	6.9	7.4	6.7	6.7	7.7	7.4
Surface conductivity (μS cm^{-1})[a]	14.6	15.0	12.0	9.2	13.0	17.0
Mean P_{tot} (SD) (μg l^{-1})[a]	6.8 (0.1)	6.6 (0.5)	7.3 (3.6)	5.2 (0.1)	4.2 (0.6)	4.3 (0.7)
Mean N_{tot} (SD) (μg l^{-1})[a]	242.2 (30.5)	225.9 (12.8)	207.4 (25.9)	198.2 (33.8)	182.3 (74.6)	149.3 (6.1)
Mean DOC (SD) (mg l^{-1})[a]	9.2 (0.3)	9.4 (0.1)	7.0 (0.3)	7.2 (0.1)	5.0 (0.1)	4.4 (0.1)
Mean Chl *a* (SD) (μg l^{-1})[a]	2.1 (0.1)	2.2 (0.2)	1.7 (0.1)	3.6 (0.3)	2.1 (0.1)	1.7 (0.1)
Biological parameters						
Yellow perch (*Perca flavescens*)	x	x	x	x	x	x
Lake chub (*Couesius plumbeus*)				x	x	
Mottled sculpin (*Cottus bairdi*)	x		x	x		
Burbot (*Lota lota*)				x	x	x
White sucker (*Catostomus commersonii*)	x	x	x	x	x	
Lake whitefish (*Coregonus clupeaformis*)		x	x			
Walleye (*Sander vitreus*)		x	x		x	
Northern pike (*Esox lucius*)	x	x	x	x	x	x

[a] Values measured in September 2003, before the perturbation (data from Winkler *et al*. 2009).

water and preserved in 4% buffered formaldehyde.

Laboratory procedure

Fish

All sampled fish were identified and preserved standard length was measured. Fish captured during the 2005 gillnet and seine samplings did not differ in length, so samples were pooled. For growth analyses, all YOY perch were selected except in lakes where more than 30 fish were captured. In these cases, a subsample was selected in such a way that the length frequency groups were sampled randomly in proportion to their numbers.

Individual growth characteristics were obtained from otolith microstructure analysis. We used the lapillar otoliths because accessory primordia and sub-daily increments are often observed in sagittal otoliths (Fig. 2). The left and right lapillar otoliths were removed under a dissecting microscope and mounted on a microscope slide with thermoplastic glue. Otoliths were polished with a 3 or 5 µm lapping film. Left otoliths were measured using an image-analysis system (SigmaScanPro 5.0) connected to a light microscope at 400–1000× magnification. Three measurements were taken along the longest axis: hatch mark radius (µm), otolith radius (µm), and individual increment widths (µm) (Fig. 2). All otoliths were analyzed twice by the same reader at an interval of > 1 month and each count estimate was ranked according to the confidence of the reading. The single best increment estimate count for all otoliths was used as the age estimation since the coefficient of variation in the number of increments counted between the first and the second reading never exceed 10% (Campana and Jones 1992). We examined 366 otoliths: 99, 63, and 204 from the 2003, 2004, and 2005 samplings, respectively (Table 2).

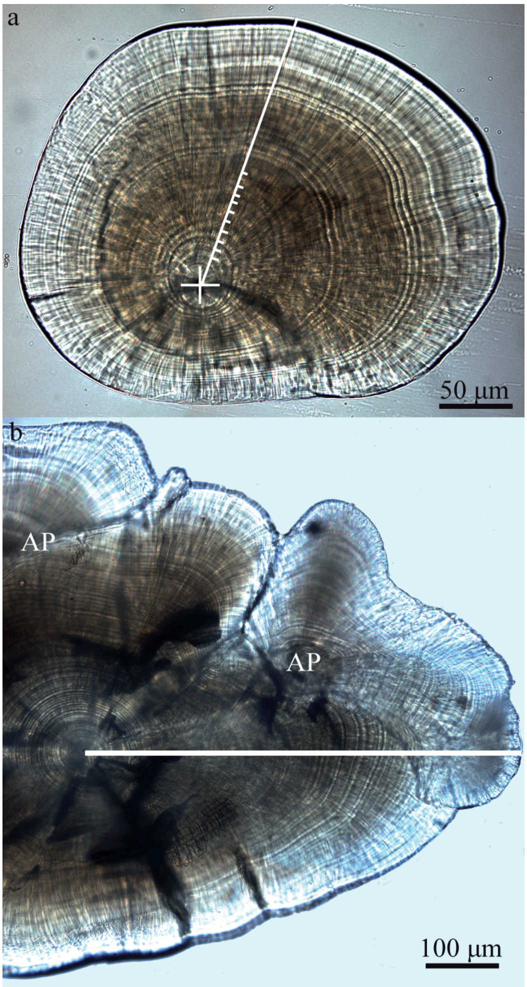

Fig. 2. Yellow perch otoliths at 400× magnification. (**a**) Lapilli of a 33.15 mm juvenile: the size of central cross indicates the hatch mark diameter, and the first 10 daily increments are highlighted with marks on the measurement axis (solid line). (**b**) Sagitta of a 44.45 mm juvenile showing accessory primordia (AP) that complicate increment measurement on the axis (solid line).

Plankton

Water samples were air-transported to the laboratory for Chl-*a* determination. A known volume of water (usually 1000 ml) was filtered through Whatman GF/C filters within 12 h of sampling. Filters were immediately frozen and kept at –80 °C until extraction according to Planas *et al*. (2000).

Zooplankton samples were treated in order to measure biomass as ash-free dry weight (AFDW, mg) per cubic meter. Samples were first sorted to remove *Chaoborus* larvae (Chaoboridae, Diptera) and divided into four equal fractions using a Folsom splitter. One quarter was used for biomass measurements on decreasing size fractions according to Patoine *et al*. (2000). Subsamples were passed through 212 μm and 53 μm sieves and then filtered onto precombusted GF/A glass fibre filters, dried for 18 h, weighed, ashed at 500 °C for 18 h, and weighed again. The organic mass was calculated as the difference between dry weight and combusted weight. According to the identification of organisms in a subsample, 212 μm size fraction was mostly composed of copepodites, adult copepods, and cladocerans. Rotifers and copepod nauplii were dominant in the 53 μm size fraction.

Data analysis

Fish

Abundance of yellow perch in each lake was estimated as the catch per unit of effort (CPUE), i.e. the number of fish per gillnet per night. YOY yellow perch growth rate over the first 40 days ($G_{0\text{–}40\text{d}}$) was computed using the equation

$$G_{0\text{–}40\text{d}} = (L_{40} - L_0)/40 \quad (1)$$

where L_{40} is the back-calculated standard length at 40 d and L_0 is the standard length at hatching as determined by the biological intercept (*see* next paragraph). Variations in growth rate were analyzed using a two-way ANOVA with lake treatment and year as factors. The principal source of variations of interest for impact assessment was the interaction between lake treatment and year. When interaction factors were statistically significant ($p < 0.05$), Tukey's HSD test was performed to identify the differences.

Fish length back-calculation methods based on otolith microstructure have to meet two criteria: (1) increments must be deposited on a daily basis, and (2) otolith growth must be proportional to fish growth (Campana 1990). It has already been demonstrated that YOY yellow perch otoliths have daily increments (Powles and Warlen 1988, Dale 2000). In addition, to support the proportionality between otolith and somatic growth, a significant positive relationship between fish length and otolith radius was observed for YOY yellow perch caught in the three years of the study in both perturbed and unperturbed (Fig. 3; $F_{1,364} = 1690.40$, $p < 0.0001$). The biological intercept procedure (Campana 1990) was then used to back-calculate length-at-age (L_t) using the equation

$$L_t = L_c + (O_t - O_c)(L_c - L_0)(O_c - O_0)^{-1} \quad (2)$$

where L is the standard fish length at the biological intercept (L_0) and at capture (L_c), and O is the otolith radius at the biological intercept (O_0) and at capture (O_c). L_0 was determined in the laboratory by measuring yolk-sac larvae newly hatched from incubated eggs collected from Lake Saint-Pierre, Quebec, Canada. A mean hatching preserved standard length of 7.53 mm (SD = 1.53, $n = 94$) and the observed individual core radius were used as the biological intercept. Growth trajectories of all fish were reconstructed using back-calculated lengths at 5-d age intervals. A onw-way ANOVA was performed to identify differences in back-calculated lengths-at-age between treatments. All analyses on length-at-age were performed on $\log_{10}$-transformed data since variance increased with age. Since lakes are the experimental units, statistical analyses on growth rates and lengths-at-age were conducted on the mean lake values.

Table 2. Sample size (*n*) of YOY yellow perch used for otolith analysis.

Year	Perturbed lakes			Unperturbed lakes			Total
	Pert.-1	Pert.-3	Pert.-5	Cont-1	Cont-3	Cont-4	
2003	12	20	19	17	14	17	99
2004	19	15	–	–	16	13	63
2005	57	43	55	11	–	38	204
Total	88	78	74	28	30	68	366

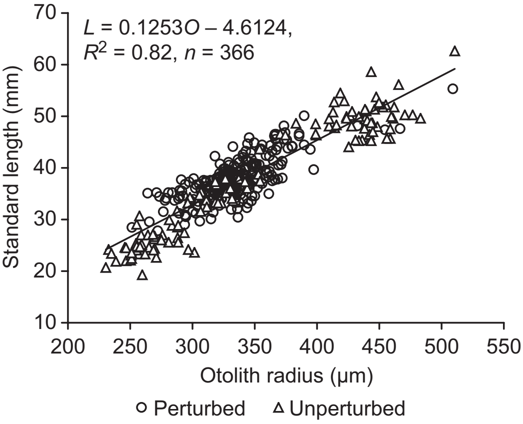

Fig. 3. Relationship between standard length (*L*) and otolith radius (*O*) of yellow perch subsampled for growth analyses in perturbed lakes and unperturbed lakes in 2003, 2004, and 2005.

Plankton

Variations in Chl *a* and zooplankton biomass were analyzed using two-way ANOVA with lake treatment and year as factors. When required, data were $\log_{10}$-transformed. In all analyses, Tukey's HSD test was performed to identify the differences when sources of variations were significant ($p < 0.05$). All statistical analyses were done using lakes as experimental units.

Results

Fish

The growth rate of yellow perch from hatching to age 40 d showed a significant interaction between lake treatment and year (Fig. 4; lake treatment × year: $F_{2,9} = 8.90$, $p = 0.0074$). In natural conditions, i.e., in unperturbed lakes, the growth rate decreased significantly from 2003 to 2005. In perturbed lakes, growth rates were similar to those in unperturbed lakes before forest harvesting but were significantly higher after the perturbation in 2005 (0.63 mm d^{-1} in perturbed lakes *vs*. 0.44 mm d^{-1} in unperturbed lakes).

Before the perturbation in 2003 as well as during the first year after the perturbation in 2004, the back-calculated lengths-at-age from ages 5 to 40 d were not statistically different between fish from both treatments (Fig. 5a and b).

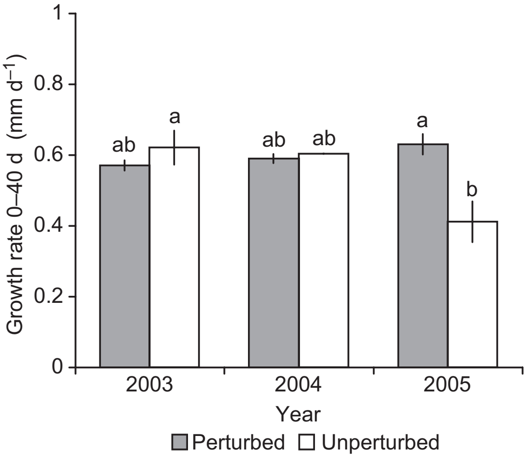

Fig. 4. Comparison between years (2003, 2004, and 2005) and treatments (perturbed lakes, unperturbed lakes) for the mean back-calculated growth rate of yellow perch from hatching until age 40 d. Vertical lines represent standard errors of mean lake values. Bars with different letters indicate groups with significantly different mean growth rates (Tukey's HSD, $p < 0.05$).

In 2005, the back-calculated lengths-at-age were higher for fish in perturbed lakes from ages 10 to 40 d (Fig. 5c: one-way ANOVA: 10 d: $F_{1,4} = 10.24$, $p = 0.0493$; 15 d: $F_{1,4} = 11.70$, $p = 0.0418$; 20 d: $F_{1,4} = 11.87$, $p = 0.0411$; 25 d: $F_{1,4} = 12.43$, $p = 0.0388$; 30 d: $F_{1,4} = 13.36$, $p = 0.0354$; 35 d: $F_{1,4} = 14.03$, $p = 0.0332$; 40 d: $F_{1,4} = 14.45$, $p = 0.0320$), emphasizing the differences in growth rates between the treatments in 2005. Fish in perturbed lakes had reached a mean back-calculated length of 32.58 mm at 40 d as compared with 25.22 mm for YOY yellow perch in unperturbed lakes.

Two years after forest harvesting, YOY yellow perch tended to be more abundant in perturbed lakes than in unperturbed ones, reaching respectively 8.2 and 1.1 CPUE in gillnets (Fig. 6). However, this difference was not statistically significant (lake treatment × year: $F_{2,12} = 2.81$, $p = 0.0999$), because the variability within treatment was very high.

Plankton biomass

A significant increase in Chl *a* was recorded in the perturbed lakes in 2005, two years after forest harvesting, whereas it remained the same

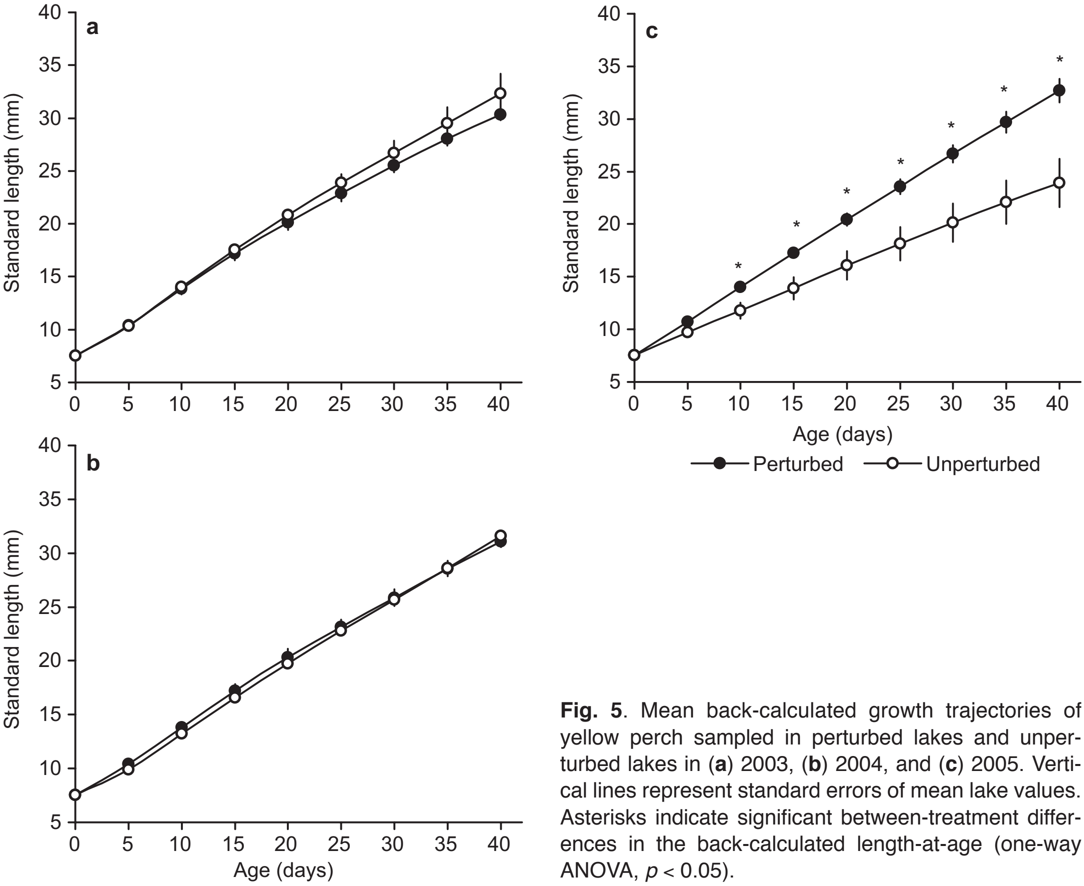

Fig. 5. Mean back-calculated growth trajectories of yellow perch sampled in perturbed lakes and unperturbed lakes in (**a**) 2003, (**b**) 2004, and (**c**) 2005. Vertical lines represent standard errors of mean lake values. Asterisks indicate significant between-treatment differences in the back-calculated length-at-age (one-way ANOVA, $p < 0.05$).

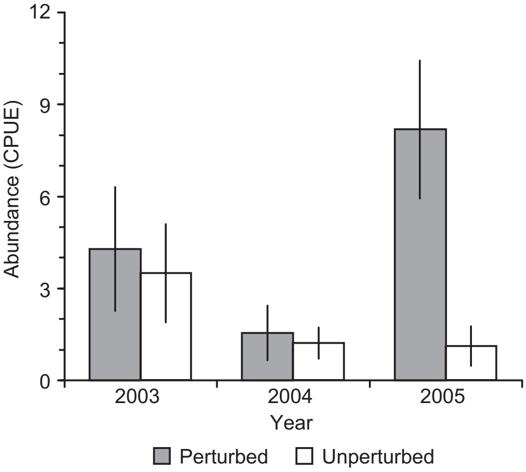

Fig. 6. Comparison between years (2003, 2004, and 2005) and treatments (perturbed lakes, unperturbed lakes) for the abundance of YOY yellow perch in experimental gillnets. Vertical lines represent standard errors of mean lake values.

among years in the three unperturbed lakes (Fig. 7a and Table 3). The mean Chl-*a* concentration in perturbed lakes was nearly two-fold higher than in unperturbed lakes in 2005 (3.90 μg l^{-1} *vs*. 1.81 μg l^{-1}).

No statistical interaction between treatment and year was detected for zooplankton biomass for either for the rotifer-nauplii size fraction or for the copepod-cladoceran size fraction (Fig. 7b and c, Table 3). Perturbed lakes had significantly higher zooplankton biomass of both size classes before and after the perturbation (Fig. 7b and c, Table 3).

Discussion

Forest harvesting effects on YOY yellow perch growth

Growth of YOY yellow perch was significantly

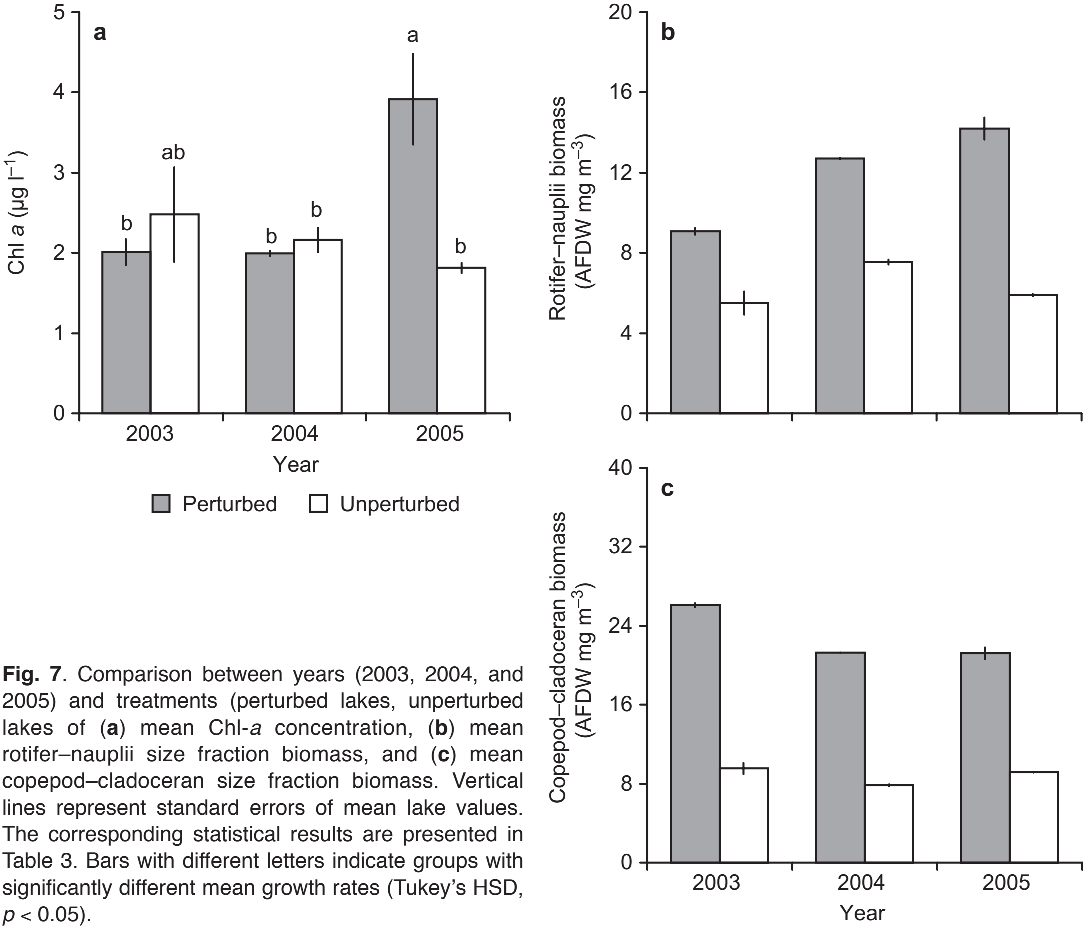

Fig. 7. Comparison between years (2003, 2004, and 2005) and treatments (perturbed lakes, unperturbed lakes of (**a**) mean Chl-*a* concentration, (**b**) mean rotifer–nauplii size fraction biomass, and (**c**) mean copepod–cladoceran size fraction biomass. Vertical lines represent standard errors of mean lake values. The corresponding statistical results are presented in Table 3. Bars with different letters indicate groups with significantly different mean growth rates (Tukey's HSD, $p < 0.05$).

higher in perturbed lakes than in unperturbed ones two years after forest harvesting. The higher growth rate of fish in perturbed lakes was observed from ages 10 to 40 d, which encompasses the complete larval stage of yellow perch in Boreal Shield lakes. Before forest harvesting,

Table 3. Results of ANOVA testing the effects of treatment (tr), year (yr), and their interaction on plankton biomass. Data were transformed as indicated.

Variable	Source	df	MS	*F*	*p*
$\log_{10}$Chl *a*	tr	1	0.13	3.02	0.1078
	yr	2	0.01	2.33	0.1394
	tr × yr	2	0.38	9.01	**0.0041**
	Residual	12	0.04		
	Total	17			
Rotifer–nauplii size fraction biomass	tr	1	144.84	30.68	**0.0001**
	yr	2	15.52	3.29	0.0727
	tr × yr	2	8.59	1.82	0.2040
	Residual	12	4.72		
	Total	17			
Copepod–cladoceran size fraction biomass	tr	1	883.82	22.45	**0.0005**
	yr	2	18.28	0.46	0.6394
	tr × yr	2	7.89	0.20	0.8211
	Residual	12	39.37		
	Total	17			

growth rates were similar in all lakes, despite some differences in productivity indices such as in turnover rate, secchi depth, DOC concentration, and zooplankton biomass. In unperturbed lakes, we observed a decrease in growth rate in 2005. Environmental conditions (temperature and precipitation) could be considered to have been the same for both lake treatments as all the lakes are interspersed within an area whose radius is less than 35 km. Since all lakes were subjected to the same interannual variations in environmental conditions except for forest harvesting in catchments, the higher growth rates and greater lengths-at-age of fish in perturbed lakes in 2005 are likely to have been caused by the perturbation. The two-years time lag in the response to forest harvesting may have been caused by a variety of factors. A combination of winter forest harvesting strategy minimizing the impact on soils, plus the buffer strips along streams and lakes, may have delayed the impact of forest harvesting (Winkler *et al.* 2009). In addition, attenuations of bottom-up effects in the trophic webs may also have contributed to the delayed response of Chl *a* and YOY perch growth (McQueen *et al.* 1986, DeMelo *et al.* 1992).

Our results suggest that fish in perturbed lakes encountered better environmental growth conditions than fish in unperturbed lakes in 2005. Early growth in fish mainly depends on temperature and feeding conditions (Anderson 1988, Jones 2002, Takahashi and Watanabe 2005, Takasuka and Aoki 2006, Robert *et al.* 2009). In YOY yellow perch, it has been reported that growth is mostly related to zooplankton biomass (Abbey and Mackay 1991, Bremigan *et al.* 2003, Clapp and Dettmers 2004, Graeb *et al.* 2004). Temperature of the study lakes remained unchanged after forest harvesting (Winkler *et al.* 2009). Hence, the observed enhanced growth in perturbed lakes was likely due to modifications in feeding conditions.

Effects of forest harvesting on lake trophodynamics

Our results on the impact of forest harvesting on Chl *a* and YOY perch growth supported the hypothesis of a bottom-up effect on lake trophodynamics. We measured a significant difference in pelagic Chl-*a* concentrations between perturbed and unperturbed lakes two years after the perturbation. We propose that an increase in nutrients due to forest harvesting, which was observed in our study lakes by Winkler *et al.* (2009) as well as in lakes examined during other studies (Rask *et al.* 1998, Carignan *et al.* 2000, Steedman 2000), may have affected Chl-*a* concentration, as has been reported in other studies (Planas *et al.* 2000, Nicholls *et al.* 2003, Ghadouani *et al.* 2006).

In other studies, forest harvesting have been shown to increase crustacean abundance (Rask *et al.* 1998) and the biomass of zooplankton $< 500\ \mu$m in size (Bertolo and Magnan 2007). In the same lakes as in this study, Winkler *et al.* (2009) observed a marginally significant increase in *Daphnia* spp. abundance in perturbed lakes following forest harvesting. No post-harvest increase in zooplankton biomass was measured in this study for the rotifer-nauplii and copepod–cladoceran size fractions. A combination of bottom-up and top-down effects may explain these results. Given that Chl *a* and YOY yellow perch growth was enhanced two years after forest harvesting, we assume that bottom-up effects may have stimulated zooplankton productivity, but may not have been measurable due to top-down control.

As observed by Bertolo and Magnan (2007), the abundance of YOY yellow perch in forest harvesting perturbed lakes tended to be higher after the perturbation. We propose that predation on zoooplankton by more abundant YOY yellow perch (Noble 1975, Mills *et al.* 1989, Schael *et al.* 1991, Wahl *et al.* 1993, Wallus 2006) may have masked an increase in zooplankton biomass in perturbed lakes. It is widely known that planktivorous fish exert a negative effect on zooplankton (Carpenter *et al.* 1987, Post and McQueen 1987, Romare *et al.* 1999, Finlay *et al.* 2007), especially when abundance is high. For example, it has been demonstrated that YOY yellow perch can strongly deplete *Daphnia pulex* populations (Mills and Forney 1983), and this could have been the case in our study.

Other considerations for fish feeding success and growth

Successful feeding results from a combination of many factors in a fish's early life, with prey abundance being one of the most important variables that determines feeding success as well as the growth and survival of young fish (Hjort 1914, Anderson 1988, Cushing 1990, Welker *et al*. 1994, Jones 2002, Houde 2008). Our results showed that perturbed lakes had naturally higher zooplankton biomass than unperturbed lakes (i.e., higher biomasses were measured before the perturbation). Despite naturally higher prey abundance, fish in perturbed lakes did not grow at higher rates before forest harvesting, suggesting that a factor other than prey biomass alone may have enhanced feeding success and growth after the perturbation. We suggest that visual feeding conditions may have been improved after forest harvesting, principally due to the observed increase in DOC after forest harvesting (Winkler *et al*. 2009).

Many studies revealed that visual feeding conditions are as much important as prey densities for the feeding success and growth in larval and juvenile fish. Turbidity has been shown to both decrease (Gregory and Northcote 1993, Wellington *et al*. 2010) and increase feeding success (Boehlert and Morgan 1985, Miner and Stein 1993, Sirois and Dodson 2000, Utne-Palm 2002, Shoji *et al*. 2005). The inconsistencies in the observed effects of turbidity on feeding success may be due to the type of turbidity involved (Utne-Palm 2002, Wellington *et al*. 2010). Independently of the type of turbidity, an enhancement of the contrast between preys and the background environment is known to increase prey detection and feeding success (Hinshaw 1985, Utne-Palm 2002). We hypothesized that elevated DOC concentrations following forest harvesting could have improved prey visibility via an enhanced contrast with the background and, consequently, led to higher growth rates for YOY yellow perch.

In conclusion, our results showed that forest harvesting enhanced YOY yellow perch growth probably via a bottom-up effect on lake trophodynamics. YOY yellow perch may benefit from the higher prey abundance, but higher prey visibility due to the increased DOC after forest harvesting may also be a factor. Our results suggest that good feeding conditions lead to fast growth for fish in perturbed lakes. According to the "growth-mortality" hypothesis, higher growth rates in early life stages after forest harvesting could favour short-term survival and recruitment in yellow perch populations.

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