

Pelagic food webs of humic lakes show low short-term response to forest harvesting

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Citation: A. Deininger, A. Jonsson, J. Karlsson, and A.-K. Bergström. 2019. Pelagic food webs of humic lakes show low short-term response to forest harvesting. *Ecological Applications* 29(1): e01813. 10.1002/eap.1813

Abstract. Forest harvest in the boreal zone can increase the input of terrestrial materials such as dissolved organic carbon (DOC) and nitrate (NO_3^-) into nearby aquatic ecosystems, with potential effects on phytoplankton growth through enhanced nutrient (i.e., positive) or reduced light availability (i.e., negative), which may affect ecosystem productivity and consumer resource use. Here, we conducted forest clear-cutting experiments in the catchments of four small, humic, and nitrogen-limited unproductive boreal lakes (two controls and two clear-cut, 18% and 44% of area cut) with one reference and two impact years. Our aim was to assess the effects of forest clear-cutting on pelagic biomass production and consumer resource use. We found that pelagic biomass production did not change after two years of forest clear-cutting: Pelagic primary and bacterial production (PP, BP), PP:BP ratio, chl *a*, and seston carbon (seston C) were unaffected by clear-cutting; neither did tree harvest affect seston stoichiometry (i.e., N:phosphorus [P], C:P) nor induce changes in zooplankton resource use, biomass, or community composition. In conclusion, our findings suggest that pelagic food webs of humic lakes (DOC > 15 mg/L) might be resilient to a moderate form of forest clear-cutting, at least two years after tree removal, before mechanical site preparation (e.g., mounding, plowing) and when leaving buffer strips along lakes and incoming streams. Thus, pelagic food web responses to forest clear-cutting might not be universal, but could depend on factors such as the time scale, share of catchment logged, and the forest practices involved, including the application of buffer strips and site preparation.

Key words: autochthony; boreal lakes; forest clear-cut; land use; light; nutrient; primary production; resource use; zooplankton.

INTRODUCTION

Forest clear-cutting is a widely used practice for managing boreal forests and has been shown to affect aquatic environments by increasing the export of dissolved organic carbon (DOC) to nearby aquatic ecosystems (Bertolo and Magnan 2007, Winkler et al. 2009, Schelker et al. 2012). High or enhanced DOC loadings may constrain pelagic primary production through shading and light absorption (Thrane et al. 2014, Seekell et al. 2015, Deininger et al. 2017a), but may also stimulate production by enhancing nutrient availability, as terrestrial dissolved organic matter (TDOM) also serves as an important carrier of nitrogen and phosphorus (P) to lakes (Jansson et al. 2001, Lennon and Pfaff 2005, Jones et al. 2012). Increasing nutrient and carbon subsidies, supplied by TDOM, might also benefit potentially

competitive organisms to phytoplankton such as bacteria (Jones 1992).

Further, forest clear-cutting has been shown to increase nitrate (NO_3^-) leakage into boreal inland waters (Likens et al. 1970, Palviainen et al. 2014, Schelker et al. 2016), with potential stimulating effects on autotrophic production in northern boreal lakes receiving low atmospheric N deposition where phytoplankton are primarily N limited (Bergström et al. 2005, Elser et al. 2009b, Deininger et al. 2017b). However, it is unclear to what extent increased N availability after forest clear-cutting might affect primary producers, since the potentially simultaneously increased DOC input and its negative effects on the light climate may counteract the positive N effect (Deininger et al. 2017a). Thus, especially in humic lakes, with high content of colored DOC in the water, the pelagic primary production response to enhanced input of limiting inorganic N may be limited (Deininger et al. 2017a).

Since forest clear-cutting has the potential to affect basal biomass production (phytoplankton and bacteria) in the pelagic habitat, it may therefore also affect their

Manuscript received 8 March 2018; revised 4 August 2018; accepted 5 September 2018. Corresponding Editor: Ryan King.

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consumers. Zooplankton growth in unproductive boreal lakes is often resource limited (Persson et al. 2007), wherefore changes in basal biomass production may directly translate into increased resource use by zooplankton consumers. However, zooplankton resource use is also strongly affected by other parameters such as food chain length, quality of resources, and species-specific feeding modes (Sterner et al. 1998, Barnett et al. 2007, Berglund et al. 2007). Thus, it is difficult to predict whether forest clear-cutting and the potentially enhanced phytoplankton biomass production will enhance the resource use of phytoplankton derived carbon by crustacean consumers in general (i.e., zooplankton autochthony), or whether net changes in zooplankton resource use will differ between taxa in accordance with their species-specific feeding modes.

The aim of this study was to assess the effects of forest clear-cutting and consequent changes in DOC and N supply to downstream lakes and how it affects pelagic biomass production and consumer resource use (degree of autochthony). For this reason, we conducted whole catchment manipulation experiments in four humic lakes (two controls, two clear-cut). We hypothesized that forest clear-cutting would induce increases in DOC and N

supply and that this would potentially enhance (1) phytoplankton production (PP), chlorophyll *a* (chl *a*), seston stoichiometry (seston C, N:P C:P), and promote a shorter food chain length. However, this positive effect would be limited by DOC-induced light limitation. (2) Therefore, we expected only small changes in zooplankton resource use of phytoplankton (i.e., autochthony), zooplankton biomass, and community composition from clear-cutting.

MATERIALS AND METHODS

Study sites

The four experimental lakes are located in boreal, northern Sweden (64.12° to 64.25° N, 18.76° to 18.80° E). All lakes have similar physical and chemical characteristics, are small (mean surface area 0.8–4.8 ha), humic (mean DOC 16–22 mg/L), and unproductive (mean chl *a* 0.7–8.3 µg/L; Table 1). All lakes are steep sided with small littoral zones where littoral aquatic vegetation generally does not extend further than ~1 m from the lake edge and not deeper than 1 m (mean littoral zone area 0.08–0.6 ha; Table 1). It consists mainly of bryophyte beds with few other macrophytes and associated

TABLE 1. Physical and chemical characteristics of the epilimnion (epi) and inlet streams (stream) of the experimental lakes in the reference year (2012) during the investigated time frame (June to September).

Parameters	Control lakes		CC lakes	
	Övre Björntjärn (Control 1)	Stortjärn (Control 2)	Lillsjöleden (Clear-cut 1)	Struptjärn (Clear-cut 2)
Lake surface area (ha)	4.8	3.9	0.8	3.1
Littoral zone area (ha)	0.3	0.6	0.08	0.2
Lake mean depth (m)	4	3	4	4
Lake maximum depth (m)	10	7	5	6
Lake water residence time (d)	63	95	115	387
Catchment area (ha)	284	82	25	79
Forest cover (%)	84	88	98	96
Mire cover (%)	16	12	2	4
Clear-cut (%)	–	–	44	18
Buffer strip width (m)	–	–	20	50
Stream discharge (L/s)	41.7	–	3.0	5.5
DOC _{stream} (mg/L)	26.7 ± 6.8	–	18.7 ± 6.4	38.0 ± 13.3
TP _{stream} (µg/L)	24 ± 9	–	13 ± 3	30 ± 31
TN _{stream} (µg/L)	457 ± 94	–	527 ± 289	730 ± 397
DIN _{stream} (µg/L)	23 ± 17	–	20 ± 15	13 ± 4
Epilimnion depth (m)	0.8 ± 0.5	0.8 ± 0.4	0.6 ± 0.3	0.8 ± 0.4
DOC _{epi} (µg/L)	21.5 ± 4.3	20.3 ± 1.9	15.7 ± 2.4	19.8 ± 4.3
TP _{epi} (µg/L)	22 ± 4	14 ± 2	18 ± 10	24 ± 5
TN _{epi} (µg/L)	398 ± 87	405 ± 68	352 ± 57	375 ± 75
DIN _{epi} (µg/L)	14 ± 9	27 ± 9	24 ± 7	16 ± 2
Temperature _{epi} (°C)	13.2 ± 3.8	13.9 ± 3.3	14.1 ± 4.3	14.5 ± 3.6
Light (<i>k_d</i>)	4.2 ± 1.5	4.4 ± 1.0	3.0 ± 0.6	3.8 ± 0.8
Light (incoming PAR, %) [†]	10.8 ± 6.1	10.5 ± 5.5	22.7 ± 11.1	13.5 ± 5.5
Photic zone depth (m) [‡]	2.4	1.8	3.1	2.3

Notes: Mean values ($n = 9$) are presented followed by standard deviations (SD). DOC, dissolved organic carbon; TP, total phosphorus; TN, total nitrogen; DIN, dissolved inorganic nitrogen; PAR, photosynthetically active radiation.

[†]Average light in the mixed water column (i.e., until thermocline depth).

[‡]Here: depth at which PAR = 1%.

epiphytes. Lake water is highly colored and light penetration is restricted to the uppermost water layers with illuminated benthic areas being limited to shallow areas close to the shorelines (Table 1). Fish were present in all lakes (mostly *Perca fluviatilis*). The lakes are ice covered from late October to early May; thermal stratification (0.5–2.0 m) occurs from late May until mid September. The lakes' catchment areas are covered mainly by managed coniferous forests (>85%; *Picea abies*, *Pinus sylvestris*) with scattered birch trees (*Betula* sp.) and open *Sphagnum*-dominated mires (<15%). Forestry is the only anthropogenic influence on the lakes, with timber productivity of 2–3 m³·ha⁻¹·yr⁻¹ (SLU 2005) indicating low site quality class. Last, the lakes are situated in an area with low atmospheric N deposition (wet dissolved inorganic N, i.e., DIN deposition <200 kg·km⁻²·yr⁻¹; Bergström et al. 2008) where previous bioassay experiments with N, P, and N + P addition have indicated strict N limitation of primary producers through the summer season (Bergström et al. 2008).

Study design and forest clear-cutting

Two lakes served as control lakes, two lakes as impact lakes (clear-cut lakes). The study reference year was 2012 (“before”; all lakes), and 2013 and 2014 were impact years (“after”, with forest clear-cutting in two of four lakes). Lake sampling was carried out biweekly from June to September ($n = 9$). During this time frame, mean epilimnion temperatures were similar in 2013 and 2014, and approximately 2°C colder in 2012. Similarly, annual precipitation was lower in 2013 and 2014 (500–600 mm) than in 2012 (800 mm). Lake light levels were similar between years (measured as the percentage of photosynthetically active radiation [PAR] available at mixing depth).

Forest clear-cutting was carried out on snow-covered (~60 cm) frozen soil in February 2013 in the catchments of the two clear-cut lakes by national or private forest companies. The trees removed came from coniferous forests with a median age of 90–120 yr. Clear-cut areas were 14 ha (Struptjärn) and 11 ha (Lillsjöleden), which corresponded to 18% and 44% of total lake watershed areas, respectively. Clear-cutting was conducted according to “common practice” methods of whole-tree harvesting where about 30% of tops, twigs, and needles are left on-site. Lake buffer strips were 15–60 m wide in both catchments, stream buffer strips were 35 m (Lillsjöleden) and <10 m (Struptjärn). All buffer strips remained widely intact throughout the study period. Site preparation of the clear-cut catchments by disk trenching did not occur during the experimental period and was conducted in early November 2014.

Sampling and analysis

Regular sampling of physical, chemical, and biological parameters was conducted biweekly at the deepest point

in each lake during the ice-free season from June to late September ($n = 9$). Samples for zooplankton stable isotopes (for consumer autochthony assessment) were taken monthly in addition to the regular lake sampling. Temperature (Temp), dissolved oxygen (O₂), and photosynthetically active radiation (PAR) profiles were measured at each sampling occasion in the lakes using handheld probes (Temp and O₂, YSI ProODO, YSI, Yellow Springs, Ohio, USA; PAR, LI-193 Spherical Quantum Sensor, LI-COR Biosciences, Lincoln, NE, USA). We calculated the vertical light attenuation coefficient k_d as the slope of a linear regression of the natural logarithm of PAR vs. depth (Kirk 2010). Assuming that vertical light attenuation followed Lambert-Beer's law, we calculated average light availability in the mixed water column (i.e., until thermocline depth) as $100[1 - \exp(-k_d z)] / (k_d z)$ as percentages of incident PAR, where z is the depth of the thermocline. Further, values for daily LUX insolation were measured using light loggers (HOBO UA-002-64, Bourne, MA, USA, 10-min logging interval) on the open shore of each lake. Composite samples for chemical and biological parameters were taken from the mid epilimnion using a Ruttner sampler. Subsamples were taken from the composite samples for analyses of water chemistry, chlorophyll *a* (chl *a*), seston stoichiometry (C:P, N:P), and bacterial production (BP).

In terms of chemical parameters, water samples were analyzed for DOC, dissolved inorganic carbon (DIC), ammonium (NH₄⁺), nitrite + nitrate (NO₂⁻ + NO₃⁻), total dissolved nitrogen as a proxy of total nitrogen (TN), and total phosphorus (TP). Dissolved inorganic N (DIN) was estimated as NH₄⁺ + NO₂⁻ + NO₃⁻. For DOC determination, samples were filtered through pre-combusted (450°C, 5 h) Whatman GF/F filters, acidified (1.2 mol/L HCl) and kept in the dark at 6°C until analysis using a HACH-IL 550 TOC-TN analyzer (Hach-Lange, GmbH Düsseldorf, Germany). For DIC analyses, 4 mL of water was sampled with a plastic syringe and injected into gas-tight glass vials (22 mL; Perkin Elmer, Boston, Massachusetts, USA) containing 50 µL 1.2 mol/L HCl and N₂. CO₂ concentrations in the vial headspace were analyzed using a gas chromatographer (Clarus 500; Perkin Elmer) equipped with a methanizer and a flame ionization detector (FID; Deininger et al. 2017b). For N and P, analysis was performed following descriptions elsewhere (Bergström et al. 2013), and samples were kept frozen until analysis. For DIN analysis (i.e., NO₂⁻ + NO₃⁻ and NH₄⁺), samples were filtered through 0.45-µm cellulose acetate filters. For TP and TN determination, aliquots of unfiltered subsamples were taken. TN was analyzed using a HACH-IL 550 TOC-TN analyzer (Hach-Lange); and TP using a flow injection analyzer (FIA star 5000; FOSS, Hillerød, Denmark) following the molybdenum blue method (ISO 1568-1) after an acid persulphate (5%) digestion in an autoclave (120°C) for 1 h. DIN:TP and TN:TP ratios are presented as molar ratios. DIN:TP ratio shall be used as an additional indicator of N vs. P limitation of primary

producers due to its higher predictive value especially in oligotrophic lakes (Bergström 2010). All chemical analyses were performed at the Department of Ecology and Environmental Science (EMG), Umeå University.

Seston (<50 µm) stoichiometry was determined by filtering known volumes of pre-filtered (50-µm mesh) epilimnion water onto GF/F filters for analysis of particulate carbon and N (pre-combusted filters at 550°C, 4 h) and P (acid-washed filters, 1.2 mol/L HCl). Particulate organic carbon and N were measured using a Costech ECS 4010 elemental analyzer (Costech International S. P. A., Milan, Italy) at the Limnology Department, Uppsala University, Sweden (Bergström et al. 2015). Filters for particulate P were analyzed as for TP (cf. above) at Umeå University (EMG). Seston C, and estimated seston C:P and N:P ratios are presented in molar.

$$\text{Autochthony}(\%) = 100 \times \left\{ 1 - \left[\frac{\delta^2\text{H}_{\text{consumer}} - \omega_{\text{tot}} \times \delta^2\text{H}_{\text{water}}}{(1 - \omega_{\text{tot}})} - \delta^2\text{H}_{\text{auto}} \right] \times (\delta^2\text{H}_{\text{allo}} - \delta^2\text{H}_{\text{auto}})^{-1} \right\}$$

For biological parameters, chl *a* was filtered onto Whatman GF/F filters and extracted for 24 h with 95% ethanol in the dark. Samples were analyzed using a luminescence spectrometer (Perkin Elmer LS45). Volumetric pelagic PP was measured using the ¹⁴C incorporation method (Schindler et al. 1972) using the same protocol outlined in (Deininger et al. 2017b). Volumetric BP was measured using the [³H]-leucine incorporation method (Karlsson et al. 2002) with modifications (Deininger et al. 2017b). Isotopes used were ¹⁴CHNaO₃ (37 MBq/mL; Perkin Elmer) for PP and Leucine (3.9 TBq mmol [06.2 Ci mmol]; Perkin Elmer) for BP. Both ¹⁴C and ³H activity were measured using a Beckman-Coulter LS6500 scintillation counter (Beckman-Coulter Inc., Fullerton, CA, USA). For PP, water samples were taken with a Ruttner sampler from five to seven depths along a depth and light profile with the uppermost five samples always at depths of 0, 0.2, 0.5, 1.0, and 1.5 m, and with two optional deeper samples spaced equally depending on the in situ light measurements. Dark control bottles were added at the surface, at 1 m depth, and at the darkest light level. Samples were incubated at sampling depth over midday (4 h). Measured PP was converted to daily rates using the ratio of PAR during the incubation period to whole day PAR. The PP:BP ratio (volumetric) was calculated for each sampling occasion using volumetric PP and BP, and is used as an indicator of food chain length, and the potential carbon sources (i.e., autochthonous vs. allochthonous carbon) used by the crustacean zooplankton consumers (Jansson et al. 2000, Berglund et al. 2007).

To estimate crustacean zooplankton biomass, vertical net hauling was performed using a 100-µm mesh net (25 cm diameter) from the deepest point of the lake (starting approximately 1 m above the lake bottom) to the surface. Samples were preserved with Lugol's iodine and kept in the dark at 6°C. Crustacean zooplankton

taxa were identified and counted using inverted microscopy (100× magnification), and the image analysis system Image Pro Plus 6.2 (Media Cybernetics Inc., Bethesda, MD, USA). Length–mass regressions (Bottrell et al. 1976) and a conversion factor of 0.48 carbon dry per mass (Andersen and Hessen 1991) were used to calculate zooplankton carbon biomass.

Autochthonous vs. allochthonous resources used by crustacean zooplankton consumers was estimated by using stable hydrogen isotopes (δ²H). We calculated the proportion of autochthonous carbon in consumer biomass (i.e., zooplankton autochthony) using a mixing model based on the δ²H of zooplankton samples (δ²H_{consumer}), the allochthonous source (δ²H_{allo}), the autochthonous source (δ²H_{auto}), and water (δ²H_{water}) as

For each trophic level, we assumed a dietary water contribution to consumer H(ω) of 0.15 ± 0.05 (mean ± SD; Cole et al. 2011, Berggren et al. 2014). Total contribution of water derived H(ω_{tot}) was calculated as ω_{tot} = 1 - (1 - ω)^τ, where τ is the number of trophic levels between the source and consumer level. Hence, we assumed τ = 1 for all cladocerans and calanoids (Wilkinson et al. 2013), and τ = 1.5 for cyclopoids, as the present cyclopoids (*Cyclops* spp.) typically have an omnivorous feeding behavior (Barnett et al. 2007) and can potentially feed on both phytoplankton as well as microzooplankton (e.g., ciliates).

We collected crustacean zooplankton for stable isotope analysis (δ²H_{consumer}) by vertically hauling a plankton net through the water at multiple sites within each lake, excluding the littoral zone. Zooplankton were stored in filtered lake water and left standing at 4°C overnight (12–24 h) for gut evacuation. Subsequently, crustacean zooplankton was separated manually into three groups: calanoid copepods (*Eudiaptomus* sp.), cyclopoid copepods (*Cyclops* spp.), and cladocerans (mainly *Ceriodaphnia* sp., *Daphnia* sp., *Bosmina* sp., *Diaphanosoma brachyurum*, *Holopedium gibberum*, and *Sida* sp.). Copepod nauplii were not included in the stable isotope analysis. Zooplankton samples were dried at 65°C, homogenized, and transferred to silver capsules. For the analysis of water δ²H (δ²H_{water}), lake surface water was filtered (0.2 µm) into airtight glass bottles without bubbles and stored at room temperature (two to six occasions for each summer and lake). Lake- and year-specific values for δ²H_{water} were included in the analysis. For the analysis of autochthonous organic matter δ²H (δ²H_{auto}), periphyton was collected monthly from a rope floating at the lake surface, as previous analysis has shown similar isotope signals of both periphyton and phytoplankton (Karlsson et al. 2012, 2015). Lake- and year-specific values were included in the analysis. For the allochthonous source (δ²H_{allo}) baseline, we used published values

measured for organic matter from the soil humus layer of the dominant vegetation types (peat, spruce, pine soils) in the same experimental area (Karlsson et al. 2015; -142.7 ± 8.9 ‰; mean \pm SD). The analysis of $\delta^2\text{H}$ of non-exchangeable H was performed at the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University, Flagstaff, Arizona, USA) following the procedure described elsewhere (Doucett et al. 2007). Solid samples were analyzed by the application of pyrolysis, and the isotopic composition of H_2 gas was measured using isotope ratio mass spectrometry. The $\delta^2\text{H}_{\text{water}}$ was analyzed using the headspace equilibration technique with H_2 gas and a platinum catalysis using isotope ratio mass spectroscopy.

Last, we estimated the autochthony of the total crustacean zooplankton community (i.e., zooplankton community autochthony) by calculating the biomass weighted mean autochthony of the different zooplankton groups (Berggren et al. 2015). Monthly available autochthony signals ($n = 4$) were interpolated to biweekly signals ($n = 9$) to match biweekly measured zooplankton biomass values, so that final community autochthony estimates would mirror community composition changes. Monthly interpolation of autochthony was based on the assumption that zooplankton autochthony changes gradually on a monthly basis.

Statistical analysis

For chemical and biological parameters, data collected biweekly during the growing season was used for statistical analysis (i.e., June to September; nine sampling occasions per year). For consumer resource use parameters, data collected monthly over the summer season were analyzed (four to five sampling occasions per year) due to the slower response times in stable isotope values of crustacean consumers compared to their food. All chemical and biological parameters except for consumers are presented as volumetric rates for the epilimnion instead of aerial rates in order to exclude possible lake morphology effects (Faithfull et al. 2011).

We evaluated the clear-cut effect on response variables (see below, same section) by comparing differences in paired sampling events before and after manipulation in the clear-cut and control lakes using mixed-effect modeling (Carpenter et al. 1989, Zuur et al. 2009). Here, we performed statistical analysis on the net responses (Δ After = After – Before) of control lakes vs. clear-cut lakes for most response variables. The approach of pairing sampling events within an experimental unit across years was chosen over pairing samples across lakes on the same sampling date, since cross-correlation analysis revealed low coherence between our reference and our treatment systems. However, this coherence is a prerequisite for detection of subtle and gradual ecological changes (cf. Kelly et al. 2016). Cross-correlation across years in the same lakes also showed low coherence. However, testing the robustness of the two statistical approaches by using simulated data revealed that the

lme approach used in this study, pairing sampling events before and after manipulation, had higher statistical power under the violation of its assumptions than the alternative approach (pairing of samples across lakes on the same sampling date; Appendix S1). In addition, testing the robustness of the statistical methods revealed that the statistical power of both approaches was strongly dependent on the strength of the treatment effect (Appendix S1). Therefore, to improve our statistical approach for detecting subtle or gradual ecological changes, a significance level of 0.1 was chosen. To account for natural between-year variation, data from 2013 and 2014 were pooled and treated as one experimental period. To correct for the nested design of our experiment (two lakes per treatment) as well as pseudoreplication over time (nine samplings per year), date nested in lake was included as a random effect in our model with treatment as explanatory variable (factors: control, clear-cut). Response variables were nutrient concentrations in stream inlets and within the lake, as well as the following biological parameters: PP, BP, PP:BP, chl *a*, seston stoichiometry (C, C:P, N:P), consumer biomass, zooplankton autochthony, and zooplankton community autochthony. Prior to all mixed-effect model analysis, response variables were inspected for normal distribution, outliers, equality of variances, and transformed when necessary to fit the requirements of ANOVA analysis (for transformations, see Tables 2, 3; no outliers were removed). *P* values < 0.1 were considered statistically significant to correct for the reduced power of our statistical analysis as described above.

To explore whether the zooplankton community composition changed after forest clear-cutting, we applied permutational multivariate analysis of variance (PERMANOVA) analysis on zooplankton community composition data on species data ($\log(x + 1)$ -transformed) and looked at the interaction of treatment with timing. To correct for the nested design of our experiment (two lakes per treatment), lake ID was included as strata in the model. Distances among the samples were computed as Bray-Curtis dissimilarities.

We performed a sensitivity analysis of the influence of the potential errors introduced by uncertainty in model parameters (ω , $\delta^2\text{H}_{\text{allo}}$, τ) on the final estimate of consumer resource use (Appendix S2). In detail, we used a Monte-Carlo procedure where we varied ω (0.15 ± 0.05 ; mean \pm SD; Cole et al. 2011, Berggren et al. 2014) and $\delta^2\text{H}_{\text{allo}}$ ($-142.7\text{‰} \pm 8.9\text{‰}$; mean \pm SD; Karlsson et al. 2015) for each sampling occasion from a normal distribution. The sensitivity analysis was conducted on the typically used trophic levels in autochthony mixing models (see above, same section), as well as on the maximum ecologically meaningful trophic levels ($\tau = 1.5$ for cladocerans and calanoids, assuming feeding on both phytoplankton and heterotrophs; $\tau = 2$ for cyclopoids, assuming pure feeding on microzooplankton; Barnett et al. 2007). Mean and SD (σ) of 5000 permutations are presented (Appendix S2).

TABLE 2. Chemical parameters of the epilimnion (Lake) and the stream inlet (Inlet) and average light in the mixed lake water column (incoming PAR, %) in the experimental lakes (means of control and clear-cut [CC] lakes) during the investigated time frame (June to September) before (2012), and after the onset of forest clear-cutting (average of 2013 and 2014).

Parameters	Control lakes		CC lakes		<i>P</i>	<i>F</i>	Cohens <i>d</i>
	Before	After	Before	After			
Lake DOC (mg/L)	20.9 ± 0.8	21.0 ± 0.5	17.7 ± 0.9	18.4 ± 0.7	0.671	0.24	0.2
Lake TP (µg/L)†	18 ± 1	15 ± 1	21 ± 2	12 ± 1	0.051	18.06	−0.9
Lake TN (µg/L)	402 ± 18	452 ± 10	363 ± 16	445 ± 15	0.237	2.78	0.4
Lake DIN (µg/L)‡	21 ± 3	15 ± 2	20 ± 2	15 ± 2	0.863	0.04	0.1
Lake TN:TP (molar)‡	54 ± 4	78 ± 6	43 ± 3	88 ± 6	0.302	1.90	0.7
Lake DIN:TP (molar)‡	2.9 ± 0.4	2.8 ± 0.5	2.5 ± 0.3	3.1 ± 0.5	0.463	0.81	0.3
Light (incoming PAR, %)†	10.7 ± 1.3	12.5 ± 0.9	18.1 ± 2.3	19.1 ± 1.4	0.825	0.06	0.0
Inlet DOC (mg/L)†	26.7 ± 1.6	25.8 ± 1.2	28.3 ± 3.3	22.8 ± 2.0	0.362	2.45	−0.5
Inlet TP (µg/L)‡	24 ± 2	38 ± 4	21 ± 5	14.7 ± 2.2	0.195	10.02	−1.0
Inlet TN (µg/L)§	457 ± 22	506 ± 22	628 ± 83	484 ± 35	0.245	6.10	−0.8
Inlet DIN (µg/L)†	23 ± 4	24 ± 2	17 ± 3	33 ± 5	0.451	1.36	0.6

Notes: Mean values are presented followed by standard errors. *P* values in boldface type indicate significant fertilization effects ($P < 0.1$) for “ΔAfter” (difference between respective value before and after clear-cutting compared to the difference in the control lakes). All $df = 1,2$.

†Values were x^2 transformed.

‡Values were square-root transformed.

§Values were x^3 transformed.

TABLE 3. Main response of biological parameters to forest clear-cutting analyzed via linear mixed effect models (LME) with random factors date, year, and lake (nested in each other).

Parameters	<i>P</i>	<i>F</i>	Cohens <i>d</i>
Chl <i>a</i> †	0.931	0.01	0.1
PP	0.656	0.27	0.1
BP	0.752	0.13	0.2
PP:BP‡	0.844	0.05	−0.1
Seston C‡	0.977	0.00	−0.2
Seston C:P	0.858	0.04	−0.1
Seston N:P	0.775	0.11	−0.1
Zooplankton community autochthony	0.795	0.11	−0.3
Zooplankton biomass	0.163	4.68	0.8

Notes: Effect size shown as Cohens *d*. All $df = 1,2$. PP, primary production; BP, bacterial production.

†Values were square-root transformed.

‡Values were x^2 transformed.

Cross-correlation analysis, mixed model statistical analyses (LME) of biological and chemical parameters and analysis of zooplankton community composition were performed in the statistical program R (R version 3.1.2; R Development Core Team 2018), using the *ccf* function and the packages *nlme* (Pinheiro et al. 2009) and *vegan* (function *adonis*; Oksanen et al. 2016), respectively. Sensitivity analysis of consumer autochthony was performed using the program MATLAB (R2016a; The MathWorks Inc., Natick, MA, USA).

RESULTS

Control and clear-cut lakes before manipulation (2012) were nutrient poor and humic (Tables 1, 2) with molar ratios of TN:TP and DIN:TP ranging from 43 to

54 for TN:TP and 2.5 to 2.9 for DIN:TP, and DOC concentrations from 17.7 to 20.9 mg/L. Lake TN:TP ratios were representative of unproductive boreal lakes with low N deposition (Elser et al. 2009a). Lake TP concentrations decreased significantly after forest clear-cutting in both clear-cut lakes (Table 2). None of the other nutrient concentrations (i.e., DOC, TN, DIN, TN:TP, DIN:TP) changed significantly following forest clear-cutting; neither were the light climate nor the inlet nutrient concentrations affected (Table 2).

Pelagic biomass production did not change after two years of forest clear-cutting: chl *a*, PP, BP, PP:BP ratio, and seston C were unaffected by clear-cutting; neither did seston stoichiometry change (i.e., N:P, C:P; Figs. 1 and 2; Table 3). Basal biological parameters were generally similar in all experimental lakes, except for chl *a*, PP, PP:BP and seston C in Struption (Clear-cut 2), which were seven-, five-, three-, and twofold higher compared to the other lakes, respectively. These high absolute values were caused by blooms of the invasive phytoplankton species *Gonyostomum semen* (Ehrenb), which occurred in all investigated years (2012–2014). This phytoplankton species was absent from the other experimental lakes.

Forest clear-cutting did not affect zooplankton resource use: neither estimated as zooplankton community autochthony nor as species-specific autochthony (Figs. 3 and 4, respectively; Table 3). The autochthony results were robust even when considering potential errors caused by uncertainties in the mixing model (Appendix S2). However, zooplankton autochthony differed between species (LME; $P < 0.001$, $F_{2,39} = 20.78$), with higher autochthony for calanoids (81 ± 29 [mean \pm SD]), than cyclopoids (59 ± 17) or cladocerans (52 ± 14). Last, forest clear-cutting did not affect total

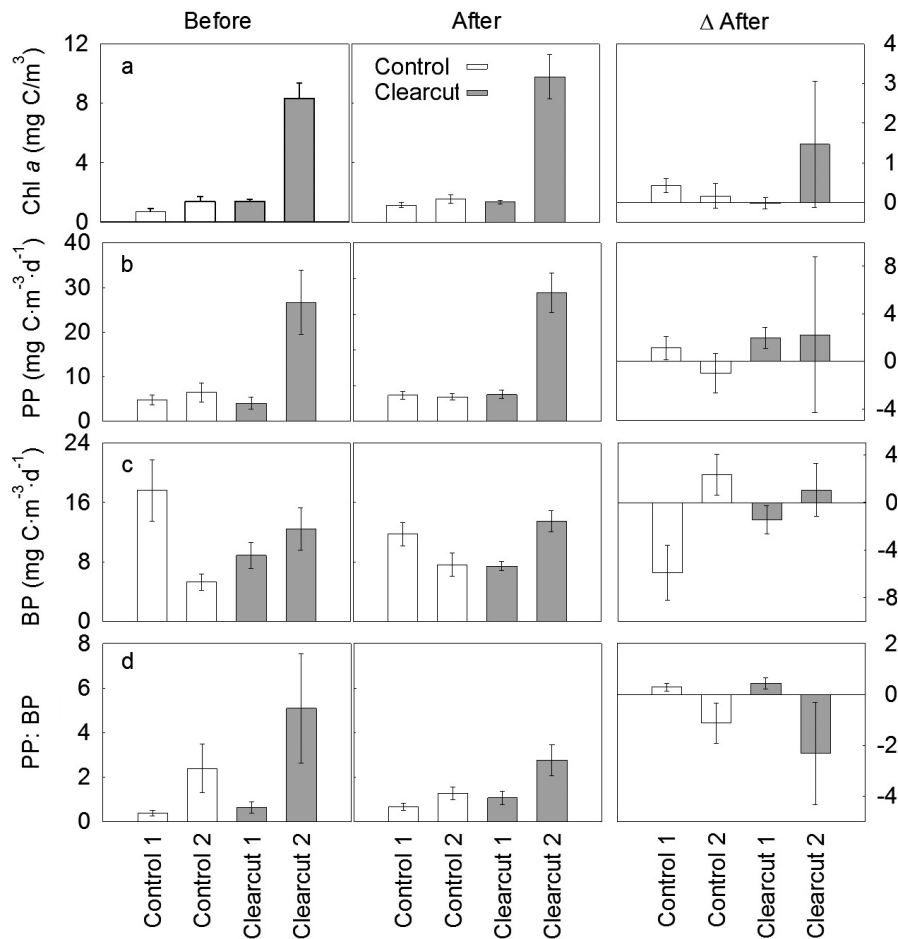


FIG. 1. Seasonal average (June to September, mean \pm SE over time, $n = 9$) of (a) chl *a*, (b) pelagic primary production (PP), (c) pelagic bacterial production (BP), and (d) the PP:BP ratio (volumetric ratio) in control lakes (white bars) and clear-cut lakes (CC, gray bars) before (2012), and after the onset of forest clear-cutting (2013 and 2014 pooled). Clear-cutting effects are presented as “ Δ After”, illustrating the difference between respective values before and after the onset of forest harvest.

zooplankton biomass or zooplankton community compositions (Table 3). In clear-cut lake 2 (Struptjärn), the bloom of *G. semen* potentially influenced results on zooplankton biomass by clogging of the zooplankton sampling net, therefore biomass results from this lake should be interpreted with caution. This is also the reason why we could not harvest enough zooplankton for isotopic analysis and autochthony assessment from this lake.

DISCUSSION

We found that, within two years after forest clear-cutting, DOC and nutrient concentrations (nitrogen and phosphorus) in stream inlets and lakes remained to a large extent unchanged, with the one exception being lower lake TP concentrations in the clear-cut lakes after forest harvest. As a result of these modest changes, neither pelagic biomass production (bacteria or phytoplankton), nor consumer resource use (degree of autochthony in zooplankton) changed in response to forest clear-cutting (rejecting both hypotheses 1 and 2).

Effects of forest clear-cutting on nutrient cycling and export rates can be highly variable in both severity and duration and are usually related to aerial extent of watershed disturbance and the proximity of harvested sites to shorelines (Ely and Wallace 2010, Kreutzweiser et al. 2013). In our study system, 18–44% of the catchments were clear-cut, which should have been enough forest removed to expect increases in nutrient runoff (Palviainen et al. 2014, Schelker et al. 2014). However, the 20–50 m wide riparian buffer strips that remained intact after clear-cutting might have been enough to stop and prevent further downstream leaching of nutrients (Kreutzweiser et al. 2013). The application of riparian buffer zones as best management practices to mitigate the impacts of forest harvesting on aquatic ecosystems is now widely implemented across both North America and Scandinavia (Kreutzweiser et al. 2013, Kuglerova et al. 2014) and has been reported to act as an important tool to effectively reduce negative effects of forestry for aquatic ecosystems (Broadmeadow and Nisbet 2004, Kuglerova et al. 2014, Laudon et al. 2016). This might

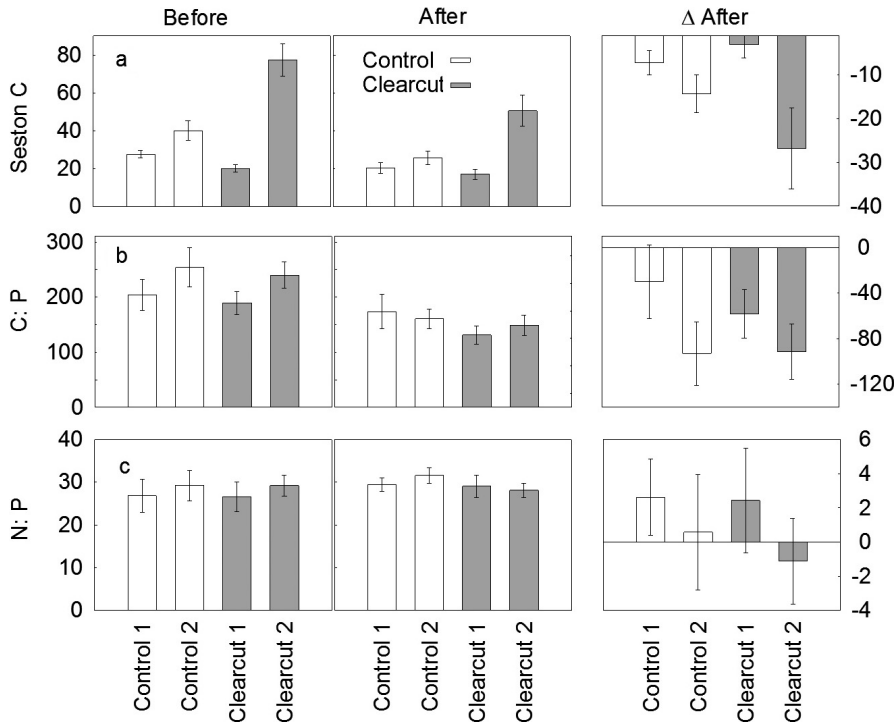


FIG. 2. Seasonal average (June to September, mean \pm SE over time, $n = 9$) of seston (a) carbon (C), (b) C:P, and (c) N:P ratio (all molar) in control lakes (white bars) and clear-cut lakes (CC, gray bars) before (2012), and after the onset of forest clear-cutting (2013 and 2014 pooled). Clear-cutting effects are presented as “ Δ After”, illustrating the difference between respective values before and after the onset of forest harvest.

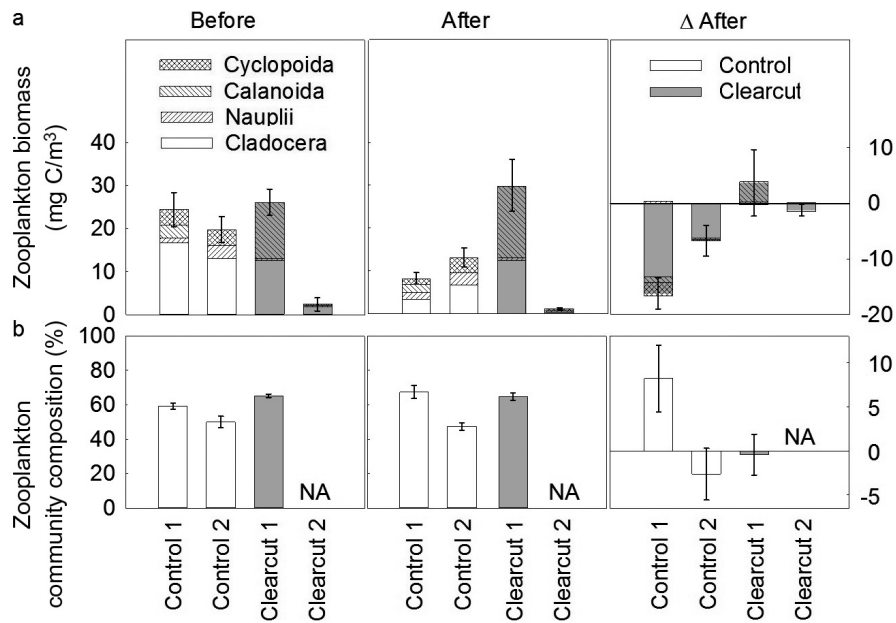


FIG. 3. Seasonal average (June to August) of (a) total zooplankton biomass (mean \pm SE over time) and (b) zooplankton community composition in control lakes (white bars) and clear-cut lakes (CC, gray bars) before (2012), and after the onset of forest clear-cutting (2013 and 2014 pooled). Clear-cutting effects are presented as “ Δ After”, illustrating the difference between respective values before and after the onset of forest harvest. NA, no values available.

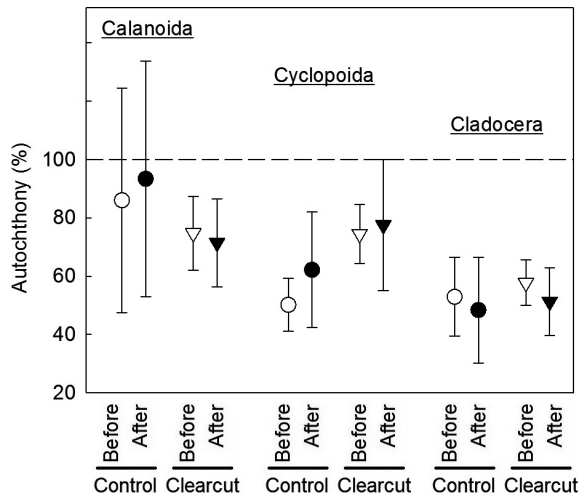


FIG. 4. Zooplankton autochthony as summer average (June to September; mean \pm SD) of calanoid copepods, cyclopoid copepods (Cyclopoida), and cladocera (Cladocera) in control lakes (circle) and clear-cut lakes (CC, triangle) before (2012; white) and after the clear-cutting (2013, 2014; black). Standard deviations illustrate seasonal fluctuations of autochthony. A figure illustrating uncertainty ranges as introduced by standard deviations of model parameters (ω ; $\delta 2H_{allo}$; τ) can be found in Appendix S2.

be especially true for nitrate in our study area, where not only pelagic but also terrestrial PP is N limited (Jansson et al. 2001, Sponseller et al. 2016, Deiningner et al. 2017b), resulting in a tight cycling of N in these low productivity forest ecosystems (Futter et al. 2016, Sponseller et al. 2016). Additionally, we cannot exclude that benthic and, especially, littoral zones might have acted as additional buffers for allochthonous material as well as nutrients entering the lakes after forest harvest. Although benthic metabolism is typically of decreasing importance for whole-lake metabolism with increasing terrestrial organic matter content and increasing light attenuation in lakes (Vadeboncoeur et al. 2008, Ask et al. 2009), littoral zones can still be important for whole-lake metabolism even in highly humic lakes (Vesterinen et al. 2017). However, the low estimated relative area covered by the littoral zone ($10\% \pm 4\%$ [mean \pm SD]; A. Deiningner, *unpublished data*), as well as the comparably high energy mobilized by pelagic vs. benthic producers ($83\% \pm 11\%$; A. Deiningner, *unpublished data*) indicate that pelagic metabolism was the major contributor to whole-lake energy mobilization in our set of lakes (Ask et al. 2009, Vesterinen et al. 2017). Supporting this hypothesis that neither littoral nor benthic processes were, to a large extent, buffering forest harvest effects on the lakes, we could not find any changes in zoobenthos resource use of primary production or terrestrial organic carbon after tree removal (A. Deiningner, *unpublished data*). Yet, a further reason for the missing response in nutrient runoff following forest harvest might be that this experiment did not include mechanical site preparation (e.g., mounding, plowing).

Site preparation has been shown to strongly increase nutrient runoff following forest clear-cutting, and nutrient runoff is often delayed until site preparation practices have started (Futter et al. 2010, 2016, Schelker et al. 2012). Last, the drier conditions in the studied impact years (2013 and 2014) with precipitation between 500 and 600 mm might be yet another reason for lower nutrient runoff (France et al. 2000, Steedman 2000).

Given that forest harvest did not affect nutrient and DOC concentrations it is not surprising that neither basal food quantities of phytoplankton or bacteria nor stoichiometry of seston were affected. We hypothesized earlier that, in humic lakes, heterotrophic bacteria should benefit most from increased carbon and P availability, resulting in increased bacterial production (Huttunen et al. 2003, Ouellet et al. 2012, Lapierre et al. 2013). However, in our experiment, bacterial production did not increase, suggesting that, besides food quantity, food chain length was also not affected by forest clear-cutting. In addition, light availability was also unchanged after forest clear-cutting as indicated by unchanged percent PAR in the mixed water column (Table 2). Thus, DOC-related reductions in light availability could not have affected photosynthesis or stoichiometric carbon content in seston as suggested by the light nutrient hypothesis (Sterner et al. 1997). Generally, theory suggests that humic lakes should be more resilient to increased nutrient inputs than clearer lakes, since pelagic PP in humic lakes is light limited, rather than nutrient limited (Thrane et al. 2014, Seekell et al. 2015, Deiningner et al. 2017a). In agreement with this theory, the phytoplankton communities in all lakes were dominated by low-light-adapted phytoplankton taxa such as the flagellated autotrophs Cryptophyceae and Chrysochyceae (A. Deiningner, *unpublished data*), which are typically found in humic boreal lakes (Klug and Cottingham 2001, Drakare et al. 2003, Deiningner et al. 2017a). In addition, we detected blooms of the flagellated microalga *G. semen*, which is invasive in Fennoscandia and has been increasing rapidly during the past 40 years (Cronberg et al. 1988, Lepisto et al. 1994) in clear-cut lake 2 (Struptionjärn). This species is also known to be well adapted to low light levels (Peltomaa and Ojala 2010) and experimental work has shown that the growth rate of *G. semen* increases with increasing DOC (Rengefors et al. 2008). Since our study lakes had DOC concentrations of more than 15 mg/L, our study only applies for humic boreal lakes. However, unproductive lakes in the boreal landscape typically vary in DOC from <5 to >20 mg/L (Downing et al. 2006, Sobek et al. 2007), where it has been observed that nutrients become a more limiting factor and light becomes a less limiting factor with decreasing DOC (Jones 1992, Seekell et al. 2015, Deiningner et al. 2017a). Therefore, clear-cutting effects on nutrient concentrations and the food web might potentially be stronger in lakes with lower DOC, having higher light availability. Indeed, a literature scan of earlier forest clear-cutting experiments in the boreal zone

indicates that, as DOC concentrations increase, phytoplankton biomass increases become less frequent, especially in stratified lakes (Table 4). However, more empirical studies are needed to investigate whether the response of “clear water” lakes to forest clear-cutting is indeed different from that of humic lakes. Further, only two of the surveyed studies addressed the response of littoral or benthic habitats to forest harvest, where both a stimulating and a neutral response to tree removal were detected (increased littoral chl *a* concentration [Planas et al. 2000] and unchanged zoobenthos resource use [Glaz et al. 2014]). Thus, this literature summary also indicates that we are far from understanding and predicting when, why, and where especially increases of phytoplankton are to occur after forest clear-cutting.

The crustacean zooplankton community did not show any response to forest clear-cutting, neither in resource use, nor in biomass or community composition. This is not surprising finding given that forest clear-cutting did not affect basal trophic levels (neither food quantity, quality, nor food chain length). Similar lack of response of crustacean zooplankton was reported from boreal Canada (Patoine et al. 2002a,b, Winkler et al. 2009). Negative effects of forest clear-cutting on zooplankton biomasses were reported earlier where forest clear-cutting increased runoff of phosphorus and induced blooms of inedible blue-green algae and decreased availability of other edible phytoplankton species (Prepas et al. 2001). However, this

is unlikely to happen in our study area where phytoplankton are N and not P limited (Jansson et al. 2001, Bergström et al. 2008, Deininger et al. 2017b), and blooms of cyanobacteria are unlikely to occur due to a combination of low TP concentrations (Downing et al. 2001), low water temperatures (Butterwick et al. 2005), and low ferric iron concentrations (Molot et al. 2014).

Considering that forestry is the predominant land use throughout the boreal zone (45°–75° N; Furukawa et al. 2015), which harbors 30% of the global forest area (Brandt et al. 2013) and the highest concentration of water bodies worldwide (Downing et al. 2006, Verpoorter et al. 2014), our study provides important insights concerning the consequences of forest clear-cutting on pelagic food webs and consumer resource use. Our study clearly illustrates that pelagic food webs of humic lakes (DOC > 15 mg/L) are resilient to forest clear-cutting up to two years after tree removal when leaving buffer strips along connected streams and lakes intact and before site preparation has been performed. However, as suggested by our literature summary, we are far from understanding which factors ultimately control food web responses to forest clear-cutting. Long-term studies, addressing both the importance of riparian buffer zone management, site preparation, and climate (precipitation and temperature) are needed (Steedman 2000, Futter et al. 2016, Laudon et al. 2016). Last, with boreal lakes facing browning with ongoing global change

TABLE 4. Impacts of forest clear-cutting (CC) on lake nutrient content, phytoplankton (Phyt.) and crustacean zooplankton (Zoopl.) in small boreal lakes.

Reference	Site	Study length	Clear-cut (%)	Buffer	DOC (mg/L)	Nutrients impact†	Phyt. parameter	Phyt. impact†	Zoopl. impact†
Paterson et al. (1998)	Ontario	30 yr	90–99	narrow/no	n.a.	n.a.	chryso. community	0	n.a.
Planas et al. (2000)	Quebec	3 yr	9–73	20 m	n.a.	+	phyt. biomass	+	–‡
Nicholls et al. (2003)	Ontario	5 yr pre, 5 yr post	45, 65	yes/no	2–3	+	phyt. biomass	+	n.a.
Patoine et al. (2002a)	Canada	1 yr	9–73	20 m	3–13	+	chl <i>a</i>	+	0,+
Hausmann and Pienitz (2009)	Quebec	5 month	~100	20 m	4–10	+	diatom community	+	n.a.
Winkler et al. (2009)	Quebec	1 yr	40–65		8–13	0,+§	phyt. biomass	0	0
Glaz et al. (2014)	Quebec	3 yr	70	20 m	11–15	0,+¶	chl <i>a</i>	0	n.a.
Prepas et al. (2001)	Alberta	2 yr pre, 2 post	0–35	20–200 m	14#	0	phyt. biomass	0	0
Prepas et al. (2001)	Alberta	2 yr pre, 2 post	0–35	20–200 m	17	+	cyano. biomass	+	–
This study	Sweden	3 yr	18–44	20–50 m	16–20	0	phyt. biomass	0	0
This study	Sweden	3 yr	18–44	20–50 m	16–20	0	phyt. production	0	0
This study	Sweden	3 yr	18–44	20–50 m	16–20	0	seston C	0	0

Notes: Chryso., chrysoytes; Cyano., cyanobacteria; n.a., information not available.

†The impact rating scale is as follows: – decrease; 0 no measurable effect; + increase.

‡Patoine et al. (2000).

§N: No effect; TP, DOC: increase.

¶First post year increase; second post year no effect.

#Stratified lakes.

||Non-stratified lakes.

(Monteith et al. 2007, Finstad et al. 2016, de Wit et al. 2016) future studies need to disentangle whether background DOC concentrations are important in predicting the response of lake ecosystems to forest clear-cutting.

ACKNOWLEDGMENTS

We thank A. Aguilar, E. Geibrink, J. Gustafson, K. Heuchel, J. Johansson, D. Karlsson, M. Klaus, W. Lidberg, L. Lundgren, M. Myrstener, S. Prideaux, and P. Rodriguez for help in field and laboratory. Forestry practices were carried out by the companies Svenska Cellulosa AB (SCA) and Sveaskog AB. We thank Karin Valinger Aggerd (SCA) and Anders Eriksson (Sveaskog AB) for help with logistics and catchment selection and the two reviewers for their valuable comments on the draft manuscript. This research received funding from Kempestiftelserna, the Swedish Research Council (dnr: 621-2010-4675) and FORMAS (dnr: 210-2012-1461). A. Deininge wrote the paper with contributions from all authors. A. K. Bergström and J. Karlsson conceived the study. A. Deininge performed the field work with support from A. Jonsson. A. Jonsson analyzed chemical samples. A. Deininge performed the stable isotope analysis, and conducted all data analysis.

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