The effectiveness of different buffer widths for protecting water quality and macroinvertebrate and periphyton assemblages of headwater streams in Maine, USA

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Abstract: We evaluated the effect of timber harvesting on water quality and macroinvertebrate and periphyton assemblages in first-order streams in Maine, USA. Fifteen streams were assigned to one of five treatments: clearcutting without a stream buffer, clearcutting with 11 m buffers, clearcutting with 23 m buffers, partial harvesting with no designated buffer, and unharvested controls. Harvest blocks on both sides of the stream were 6 ha and partial harvesting within buffers was allowed. Specific conductivity, pH, dissolved oxygen, turbidity, and soluble reactive phosphorus did not change significantly for 3 years after harvesting in all treatments. Unbuffered streams had significantly elevated concentrations of chlorophyll *a* as well as increased abundance of algal feeding organisms (Diperta *Cricotopus* and Diptera *Psectrocladius*). Streams with 11 m buffers had substantial (10-fold) but nonsignificant increases in chlorophyll *a*. No other significant changes were detected in other treatment groups. In all treatment groups, the dominant taxa (periphyton *Achnanthes minutissimum* and macroinvertebrate Chironomidae) are adapted to disturbed environments. We attribute the limited harvest-induced changes to lack of soil disturbance within 8 m of the stream, the small (≤40%) proportion of watersheds harvested, and the resilient nature of aquatic organisms. However, small-scale changes may not be detected due to the small sample size, an inherent limitation of field-based studies.

Résumé : Nous évaluons les effets de la récolte du bois sur la qualité de l'eau et sur les communautés des macroinvertébrés et du périphyton dans des cours d'eau d'ordre un dans le Maine, É.-U. Quinze ruisseaux ont été soumis à l'un de cinq traitements : coupe à blanc sans zone tampon riveraine, coupe à blanc avec zone tampon de 11 m, coupe à blanc avec zone tampon de 23 m, récolte partielle sans zone tampon désignée et témoin sans coupe. Les blocs de coupe des deux côtés du ruisseau couvraient 6 ha et la coupe partielle était permise dans les zones tampons. Dans tous les traitements, il n'y a eu aucun changement significatif dans la conductivité spécifique, le pH, l'oxygène dissous, la turbidité et le phosphore réactif soluble au cours des 3 années qui ont suivi la récolte. Les ruisseaux sans zone tampon avaient des concentrations significativement plus élevées de chlorophylle *a*, de même qu'une abondance accrue d'organismes consommateurs d'algues (diptères *Cricotopus* et diptères *Psectrocladius*). Les ruisseaux avec des zones tampons de 11 m ont connu des augmentations de l'ordre de 10 fois, bien que non significatives, de la chlorophylle *a*. Aucun changement supplémentaire n'a été décelé dans les autres traitements. Dans tous les groupes expérimentaux, les taxons dominants (*Achnanthes minutissimum* dans le périphyton et les Chironomidae chez les macroinvertébrés) sont adaptés aux environnements perturbés. Nous expliquons les changements modestes induits par la récolte du bois par l'absence de perturbation du sol à moins de 8 m du ruisseau, au faible pourcentage (≤40%) du bassin versant soumis à la coupe et à la nature résiliente des organismes aquatiques. Cependant, il est possible que des changements à petite échelle n'aient pas été détectés à cause de la taille réduite des échantillons, une limitation inhérente aux études de terrain.

[Traduit par la Rédaction]

Introduction

The importance of maintaining the ecological integrity of surface water has resulted in a greater scrutiny of timber operations adjacent to watercourses. Disturbance related to timber harvesting can change the physical, chemical, and biological composition of streams. Timber harvesting near stream channels can result in increased sediment and fine particles in the stream channel (Golladay et al. 1987; Waters 1995; Kreutzweiser and Capell 2001), acidification (Hornbeck 1992), and increased conductivity (Hornbeck et al.

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1987) of stream water. Increased in-stream sediment from forestry practices can change physical habitat (MacDonald et al. 1991) and alter species composition of macroinvertebrate (Stout et al. 1993; Waters 1995) and periphyton (Bottorff and Knight 1996; Kiffney et al. 2003) communities. Harvesting of riparian trees reduces shade and increases levels of solar radiation reaching the stream channel (Sullivan et al. 1990). This resulted in increased water temperature (Brown and Krygier 1970; Wilkerson et al. 2006), increased levels of primary productivity in the stream (Murphy 1998; Kiffney et al. 2003), and decreased levels of dissolved oxygen (Beitinger and Fitzpatrick 1979).

A key strategy for protecting water bodies from the effects of timber harvesting is the retention of riparian buffers. Riparian buffers reduce sediment by stabilizing soil on upland slopes and stream banks (Richardson 2004), reducing the velocity of overland flow (Castelle et al. 1994), and trapping mobilized soil particles (Brown and Binkley 1994). Forested buffers also shade the stream channel from solar radiation (Brown and Krygier 1970).

Headwater streams can account for 65%–75% of the cumulative length of all stream and river channels in a watershed (Leopold et al. 1964). Small headwater streams (intermittent and small first-order) often lack regulatory mandates for riparian buffers (Sidle et al. 2000). For example, in the State of Maine, buffers are not required for streams draining watersheds less than 121 ha (Maine Department of Conservation 1999). Establishing buffers on these streams could substantially reduce or eliminate timber harvesting from a significant amount of land (Bren 1995) and increase the cost of environmental protection for landowners (Shaffer et al. 1998; Cubbage 2004; LeDoux and Wilkerson 2006).

However, science has increasingly demonstrated the vital ecological role of small streams (Gomi et al. 2002). It is important that landowners protect headwater streams, but buffers that are wider than necessary result in unnecessary economic loss to the landowner (Castelle and Johnson 2000). More information is required to accurately determine the buffer width necessary to maintain the physical, chemical, and biological characteristics of headwater streams. In an earlier publication, we evaluated the effectiveness of different buffer widths for protecting stream temperature (Wilkerson et al. 2006). In this paper, we assess changes in water chemistry (conductivity, pH, dissolved oxygen, soluble reactive phosphorus concentrations, and turbidity) and periphyton and macroinvertebrate assemblages following timber harvesting on streams without buffers and with partially harvested buffer strips of various widths.

Materials and methods

Study area

The study area in western Maine is characterized by moderately rugged forested topography with numerous streams, rivers, and lakes. Elevation ranges from 900 to 1300 m. The primary land use is forestry, with large tracts of land managed primarily for timber products. The forest is typical of the Acadian Forest Region (Seymour and Hunter 1992) consisting of northern hardwood, spruce–fir, and mixed hardwood–conifer stands. Forest types of the study sites have been previously described in Hagan et al. (2006) and Wilkerson et al. (2006).

Study layout and sampling regime

We selected 15 headwater (first-order) streams within a 100 km radius of 45°00′00″N, 70°20′00″W (Fig. 1). Stream geomorphology was typical of streams in mountainous terrain. Channels were incised (Hagan et al. 2006) and the dominant channel substrate was predominately boulders and cobbles. Each stream drained small watersheds (30–195 ha) with mature forest (canopy cover >85% and tree height at least 15 m tall) without recent (>20 years) logging activity. Tree basal area at study sites ranged from 20.4 to 33.9 $m^2 \cdot ha^{-1}$ (Wilkerson et al. 2006). Along each stream, we established 500 m study segments with the downstream end of the segment at least 20 m upstream from any human disturbance (e.g., logging roads or timber harvests). We permanently marked the study reach so the same points could be measured each year.

The experiment has a replicated before–sfter–control–impact (BACI) design (Stewart-Oaten et al. 1986; Smith et al. 1993; Underwood 1994). Data were collected each year at both treatment and control sites both before and after the treatments were applied. Pre-treatment sampling established the relationship between the treatment sites and the control sites. In the pre-treatment year, there were no significant differences among treatment groups in any water quality parameters ($p > 0.127$). After pre-treatment sampling in 2001, 200 m by 300 m (6 ha) blocks on each side of the stream channel were harvested (except for controls, Fig. 2). The harvest blocks were adjacent to 300 m of stream channel. Undisturbed forest (within the last 20 years) was maintained upstream of the harvest zone in all years of the study.

We strived to apply a rigorous, well-replicated field experiment that investigated the impacts of timber harvesting on water quality of small headwater streams. However, a limitation of large field experiments such as this one is the modest sample size within each treatment. This study may lack sufficient statistical power to detect small impacts on water quality and aquatic assemblages. To minimize this limitation, we selected a suite of physical, chemical, and biological parameters that had been shown by other researchers to be sensitive to timber harvest activity.

We collected data for each parameter both upstream of the harvest block (upstream station, Fig. 2) and at the downstream boundary of the harvest block (harvest station, Fig. 2). Hereafter, the sampling station upstream of the harvest block will be referred to as the upstream station and the station within the harvest block will be referred to as the harvest station. Samples taken at the upstream and harvest stations allowed comparison between harvested and undisturbed portions of each stream.

Each study stream was randomly assigned to one of five treatment groups: (*i*) clearcut harvest (post-harvest basal area <6.8 $m^2 \cdot ha^{-1}$) leaving no buffer (0 m treatment), (*ii*) clearcut harvest with 11 m buffers on both sides of the stream (11 m treatment), (*iii*) clearcut harvest with 23 m buffers on both sides of the stream (23 m treatment), (*iv*) selection cut harvest retaining at least 13.7 $m^2 \cdot ha$ residual

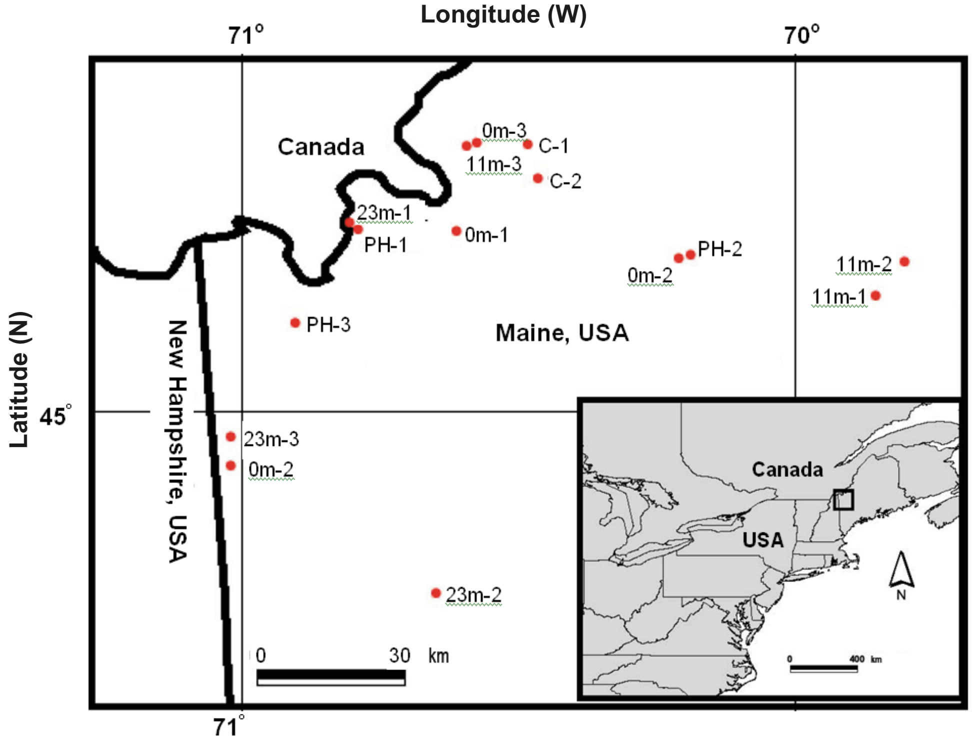

Fig. 1. Location of the study area and study streams in western Maine, USA. Individual sites are coded according to treatment group (0m, no buffer; 11m, 11 m buffer; 23m, 23 m buffer; PH, partial harvest; C, control) and individual site number (1, 2, or 3).

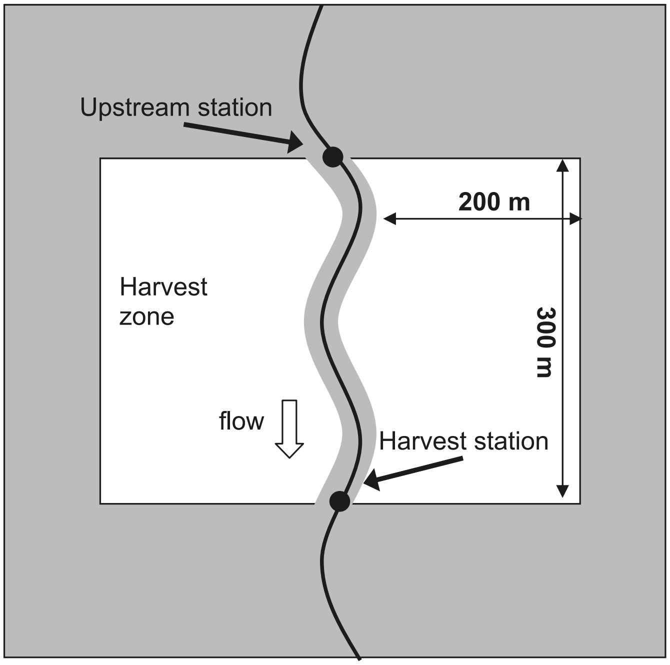

Fig. 2. Layout of study segments and harvest zones for each of 15 streams. The three control streams did not have a harvest zone.

basal area^{-1} in the harvest zone, without a specified buffer width (partial harvest treatment), and (*v*) unharvested (control treatment). Partial harvesting (retention of >13.7 m^2·ha basal area^{-1}, about 60% of a fully stocked stand) was allowed in all buffers because timber removal within buffer zones is permitted and is a common practice in Maine. The size of the harvest blocks was the same for all treatment groups. Because watershed size varied among study streams, the percentage of the watershed harvested varied by study stream (Table 1), but it did not vary significantly among the treatment groups (p = 0.293).

We strived to make the study design as representative as on-the-ground management practices as possible. The 6 ha harvest blocks were similar in size to other commercial clearcut harvests in Maine (mean size = 8 ha; Maine Forest Service 2006). The 0 m treatment reflected the most extreme harvest treatment permitted by law. The 23 m treatment corresponds with existing state buffer width requirements for higher order streams (Maine Department of Conservation 1999). We included an 11 m treatment (approximately one half of 23 m) as an intermediate treatment between these two harvest treatments. The partial harvest treatment group was also included because selection harvest techniques (e.g., overstory removal, shelter wood) are becoming more common than clearcutting in Maine (Maine Forest Service 2006).

Loggers were required to adhere to two best management practices (BMPs): (*i*) no soil disturbance or compaction within 8 m of the stream channel and (*ii*) avoid or use temporary bridges for all stream crossings. Trees could be removed within 8 m of the stream channel as long as logging equipment did not compact or disturb soils. Haul roads and stream crossings can also be large sources of sediment to water bodies (Rothwell 1983; Martin and Hornbeck 1994) but they were not a factor in this carefully designed harvest experiment.

Physical measurements

Bankfull width, gradient, and canopy closure measurements were taken every 20 m and averaged over the study

Table 1. Physical characteristics of 15 study sites in western Maine, USA.

Stream	Elevation (m)	Watershed area (ha)	% of watershed harvested	Mean discharge (SE) ($L \cdot s^{-1}$)	Mean gradient (min, max) (%)	Mean bankfull width (min, max) (m)
0m-1*	637	30	40	8.2 (3.3)	15 (4, 31)	1.9 (0.9, 4.0)
0m-2	469	52	23	3.5 (1.0)	11 (3, 19)	2.5 (1.0, 6.5)
0m-3	616	41	29	8.8 (2.2)	12 (9, 17)	3.1 (1.3, 5.5)
11m-1†	345	96	13	1.3 (0.4)	10 (5, 17)	3.9 (2.3, 5.8)
11m-2*	408	80	15	3.4 (0.8)	7 (0, 19)	2.8 (1.3, 6.1)
11m-3	619	37	32	2.9 (0.8)	12 (12, 20)	2.0 (0.7, 4.8)
23m-1	628	53	23	11.1 (3.7)	13 (3, 25)	2.6 (1.3, 5.1)
23m-2	371	67	18	10.6 (3.5)	6 (2, 11)	2.4 (1.1, 3.4)
23m-3*	462	185	6	19.5 (3.0)	9 (2, 14)	3.8 (2.2, 6.5)
PH-1	598	58	21	11.1 (3.2)	12 (5, 31)	2.0 (0.8, 4.9)
PH-2	436	44	27	3.1 (0.9)	18 (10, 31)	2.3 (1.1, 5.2)
PH-3*	647	140	9	19.5 (2.4)	5 (2, 7)	4.5 (2.1, 13.2)
C-1†	687	82	0	25.4 (7.5)	13 (6, 19)	2.8 (1.4, 4.7)
C-2	455	71	0	4.7 (1.1)	11 (3, 16)	3.6 (2.6, 5.5)
C-3	577	195	0	22.4 (2.9)	11 (3, 17)	4.2 (2.4, 7.6)

*Location of taxonomic analysis of periphyton preformed.
†Site excluded from macroinvertebrate analysis.

segment. We measured stream flow using a current velocity meter (Swoffer model 2100; Swoffer Instruments, Seattle, Washington). Measurements were taken along a cross section of the stream channel (Gallagher and Stevenson 1999) at the harvest station (Fig. 2) during three visits between 19 May and 25 June of each year. Physical parameters (listed in Table 1) did not vary significantly by treatment group ($p > 0.091$), indicating that physical parameters were well distributed among the treatments. Precipitation was measured using a data logging rain gauge (Onset Corporation, Bourne, Massachusetts) that was deployed near study site 0m-1 (Fig. 1). After the harvest (in 2002), we assessed the occurrences of soil disturbance within 8 m of the stream channel. We recorded the frequency of exposed mineral soil and attributed a source to each occurrence (logging activities (e.g., equipment tracks, skid trails), natural processes (e.g., overland flow, stream overflow/flooding), and undetermined activities (e.g., could not be confidently attributed to another category)).

Temperature measurements

At each study stream, water temperature was measured hourly between 15 June and 15 August of each year using automatic data loggers (OnSet Optic StowAway temperature loggers; Onset, Inc., Bourne, Massachusetts; error ±0.2 °C). Methods and results for stream temperature have been previously described (Wilkerson et al. 2006). In this paper, we briefly summarize water temperature changes observed between the upstream and harvest stations to help explain some of the post-harvest changes in water quality and biological communities.

Water quality measurements

Water quality measurements were collected between 19 May and 25 June in the pre-harvest year (2001) and three post-harvest years (2002–2004). Each stream was sampled on three separate visits in the pre-harvest year (2001) and in post-harvest years 2002 and 2003. In the third post-harvest year (2004), each stream was only sampled twice because we did not observe changes in water quality in the first two post-harvest years. During each visit, three readings (replicate samples) were taken at both upstream and harvest stations (Fig. 2). Readings at each station were averaged for analysis. In situ measurements of specific conductivity (error ±1%), pH (error ±0.2), and dissolved oxygen (error $\pm 0.2\ mg \cdot L^{-1}$) were made using handheld Hydrolab Quanta units (Hydrolab Corporation, Loveland, Colorado). In-stream turbidity was measured using a handheld LaMotte Turbiditimeter 2020 (LaMotte Corporation, Chestertown, Maryland; error ±2%). Both water chemistry and turbidity were measured in representative, well-mixed portions of the stream.

Methods for collection of soluble reactive phosphorus (SRP) and chlorophyll *a* samples were adapted from Maine Department of Environmental Protection protocols (Danielson 2003). Samples were collected at upstream and harvest stations (Fig. 2) between 8 and 20 July in the pre-harvest year (2001) and two post-harvest years (2002–2003). Water samples for SRP analysis were collected in laboratory sealed sample bottles (250 mL acid-washed Nalgene bottles; Nalge Nunc International, Rochester, New York) from a well-mixed portion of the stream.

Chlorophyll *a* and periphyton species

Chlorophyll *a* samples were taken from natural substrate (rocks). Collection occurred at upstream and harvest stations (Fig. 2) between 8 and 20 July in the pre-harvest year (2001) and two post-harvest years (2002–2003). At each location, 18 rocks were randomly selected from well-mixed representative areas of the stream channel. A fixed area delimiter ($5.1\ cm^2$) was securely placed on each rock and the portion of the rock within the delimiter was vigorously scrubbed with a toothbrush. Distilled water was used to rinse material into opaque plastic bottles (500 mL Nalgene Amber Bottles). Samples were stored on ice and analyzed by the Maine state Health and Environment Testing Laboratory

(Augusta, Maine) according to standardized procedures (Danielson 2003).

Taxonomic analysis of periphyton samples was expensive and therefore collected from only one stream in each of the 0, 11, and 23 m and partial harvest treatment groups (Table 1). Periphyton were collected using the same methods and at the same time and locations as for chlorophyll *a*. A preservative (M3) was added to the sample (1 mL of M3 for 50 mL of sample volume). Species identification of diatoms and other algae was performed by Michigan State University taxonomists under contract with the Maine Department of Environmental Protection.

Macroinvertebrates

Macroinvertebrates were sampled in the second post-harvest year (2003), after the study sites were exposed to a full year of post-harvest conditions, according to methods adapted from Davies and Tsomides (2002). Plastic mesh bags (mesh diameter of 2.54 cm) were filled with 7.25 ± 0.5 kg of rocks 3.8–7.6 cm in diameter. Although Davies and Tsomides (2002) sampled during the summer low-flow period (1 July to 30 September), stream flow at that time of year in our streams would not sufficiently cover the rock bags. Therefore, we sampled in June when water levels covered the rock bags.

Six rock bags were placed in each stream; three rock bags were deployed at both upstream and harvest stations (Fig. 2). The bags were deployed for 33–36 days to allow time for macroinvertebrate colonization and collected between 24 and 30 June. The bags were removed from the streams using an aquatic sampling net (mesh size 500 µm). All material (macroinvertebrates, leaf litter, and detritus) was separated from the rocks in a mesh-bottom bucket (mesh size 500 µm) and then placed in plastic sample bottles (Nalgene, various sizes) and preserved with 70% ethanol. The samples from each rock bag were pooled to form one sample for each sampling station (upstream or harvest). The samples were analyzed by Ecoanalysts, Inc. (Moscow, Idaho). A subsample of 300 individuals was selected; these specimens were identified to genus for Diptera and to the lowest possible taxonomic level for the remaining taxa.

Data analysis

Daily and yearly variations in rainfall, weather patterns, nutrient concentrations, and discharge volume of the stream can influence water quality parameters (Dissmeyer 1994). Data collected from upstream stations were unaffected by timber harvest activities and only influenced by natural variations, whereas data collected from downstream stations were influenced by both harvest impacts and natural variation. Comparing the difference in water quality parameters collected from the two stations (downstream station minus upstream station) at each stream before and after the harvest allowed us to distinguish between changes due to natural variation versus the harvest treatment and account for variation among streams.

Statistical analyses: water quality and chlorophyll *a*

We used repeated-measures analysis to examine differences among buffer treatments for the various dependent variables over time (PROC MIXED; SAS Institute Inc. 1999). Treatment and Year (one pre-harvest year, two or three post-harvest years) were both independent variables, and Year was the repeated variable in the analysis. An interaction term (Treatment × Year) could indicate a differential effect of year (pre- versus post-harvest) on the various buffer prescriptions. Because one treatment was a control (no harvest) and because the buffer treatments were quite different from one another, the interaction term would be statistically significant if harvesting had a significant effect on water quality variables. When the interaction term (Treatment × Year) was significant, we used the Dunn's test (Dunn 1961) to analyze for effects among buffer treatments within a year. The Dunn's test analyzes differences between the pre-treatment and post-treatment means within each treatment group using Bonferroni-adjusted multiple *t* tests (Howell 1982).

Table 2. Number of occurrences of exposed mineral soil less than 8 m from the stream channel within the 300 m harvest zone as a result of logging activities, natural processes, or undetermined source.

Treatment	*n*	Logging	Natural	Undetermined
0 m	3	7	36	5
11 m	3	8	74	14
23 m	3	3	41	3
Partial harvest	3	5	106	2
Control	3	0	65	6
Total	15	23	322	30

Statistical analysis: macroinvertebrates

An analysis of variance (ANOVA) (PROC GLM; SAS Institute Inc. 1999) was used to evaluate the buffer treatments on macroinvertebrate assemblages in the second post-harvest year (2002). Buffer treatment was the independent variable and the dependent variable was the difference between the upstream and harvest stations (harvest station minus upstream station) for selected community metrics including abundance, species richness, Shannon–Wiener diversity index (Shannon and Weaver 1949), and Simpson's heterogeneity index (Simpson 1949). Indicator species analysis (Dufrêne and Legendre 1997) was used to identify taxa that showed differential occurrence among the treatment groups (PC-ORD version 4.25: McCune and Mefford 1999; McCune and Grace 2002). Analysis of the macroinvertebrate assemblage was performed on 13 of the 15 study streams in the second post-harvest year (2003). One control stream (C-1) and an 11 m buffer stream (11m-1) were removed from the analysis due to very low stream flow or partial drying of the stream segment at one or more of the sampling locations.

Results

Pre- and post-harvest forest conditions

A post-harvest assessment showed that loggers applied the required BMPs within 8 m of the stream channel. In all treatment groups, only 23 occurrences (6% of total) of exposed mineral soil were attributed to logging (Table 2). The majority (322, 86% of total) of occurrences of exposed mineral soil were attributed to natural processes primarily scour-

Table 3. Total rainfall and frequency of rainfall events between 15 June and 15 August in the pre-harvest and three post-harvest years.

	Pre-harvest	Post-harvest year 1	Post-harvest year 2	Post-harvest year 3
Total rainfall (cm)	14.07	20.35	16.64	21.69
Rainfall frequency ($cm{\cdot}day^{-1}$)				
<1.00	19	18	16	27
1.00–2.00	6	7	3	6
2.00–3.00	1	2	2	1
>3.00	0	1	1	1

ing of soil during storm events (overland flow and flood events). Stream canopy cover was reduced 57%–62% in the 0 m treatment group following the harvest (Wilkerson et al. 2006). Stream canopy cover was not reduced further because loggers occasionally left residual trees to avoid compromising the stream bank or disturbing near-stream soils. Canopy closure changes averaged –3% to –8% in the 11 m treatment group and no changes occurred in the 23 m or partial harvest treatment group (Wilkerson et al. 2006). Partial removal of timber within buffers averaged 21%–31% of pre-harvest basal area (Wilkerson et al. 2006).

Stream flow and precipitation

Average spring stream flows ranged from 1.3 to 2.5 $L{\cdot}s^{-1}$ (Table 1). We do not have continuous stream flow data, but from the rainfall data, we can infer the frequency of storm events in our region. Between 15 June and 15 August in the pre-harvest year (2001) and three post-harvest years (2002–2004), rainfall totals ranged from 14.1 to 21.7 cm (Table 3). About 70% of rain evens resulted in <1 cm of rainfall in a 24 h period (Table 3). These small, frequent rain events could increase stream flow above base conditions but did not result in extreme flow events. Extreme rainfall events within a 24 h period were infrequent but in each year included one or more rain events that exceeded 2 cm within 24 h (Table 3). Storm events exceeding 3 cm in 24 h occurred once in each of the three post-logging years (Table 3). Extreme rainfall events delivered by an intense summer storms would result in a high-flow event.

Stream temperature

Following the harvest, mean weekly maximum temperatures increased significantly in the 0 m treatment group (1.4–4.4 °C) at the harvest station (Wilkerson et al. 2006). No significant post-harvest temperature changes were observed in the 11 m (+1.0 to +1.4 °C), 23 m (–0.5 to +0.5 °C), partial harvest (–0.1 to +1.0 °C), or control (–0.3 to +0.5 °C) treatment groups. Despite the post-harvest temperature increases in the 0 m treatment group, average mean weekly maximum temperatures at the harvest station did not exceed 17 °C (Wilkerson et al. 2006), well below the critical temperature threshold for brook trout (*Salvelinus fontinalis*) of 24 °C (Environmental Protection Agency 1986). Detailed temperature results are presented in Wilkerson et al. (2006).

Water quality

Water quality values from the harvest station give a reference point to the physical, chemical, and biological properties of the study streams and also show the range of post-harvest changes (see Appendix A for values). Differences in water chemistry parameters between the upstream and harvest stations were small (Table 4) and did not statistically vary among treatments and years (pH ($F_{[12]} = 1.74$, $p = 0.107$), conductivity ($F_{[12]} = 1.09$, $p = 0.399$), dissolved oxygen ($F_{[12]} = 1.02$, $p = 0.460$), and turbidity ($F_{[12]} = 0.70$, $p = 0.738$)).

SRP is primarily composed of orthophosphate (PO_4^{3-}) (Dodds 1995), which is the most readily available source of phosphorus to algae and plants (Shortreed and Stockner 1983). Statistical analysis of the changes in SRP concentrations between harvest and upstream stations showed no significant interaction between treatment and year ($F_{[8]} = 0.47$, $p = 0.857$), indicating that buffer treatments did not affect SRP concentrations in our study streams. There were no large changes in SRP concentrations between sampling stations (Table 5). Average SRP concentrations at the harvest stations were very low (<0.007 ppm) (Appendix A).

Chlorophyll *a*

The difference in chlorophyll *a* concentrations between the harvest and upstream station showed a significant interaction between treatment and year ($F_{[8]} = 2.83$, $p = 0.037$). Thus, one or more buffer treatments may have had an effect on chlorophyll *a* concentrations (the control was not expected to change). An analysis of the main effects showed that in the second post-harvest year (2003), differences in chlorophyll *a* concentrations between sampling stations were significantly greater than pre-harvest values in the 0 m treatment group ($p = 0.042$) (Table 5, Dunn's test). Thus, chlorophyll *a* concentrations increased after harvesting in the 0 m treatment group in the second post-harvest year (2003). In the 11 m treatment group, average chlorophyll *a* concentrations increased over 10-fold within the harvest zone in the second post-harvest year (Table 5). These increases are not significant ($p > 0.05$) but indicate that algal biomass increased within 11 m buffers. No significant changes were observed in the first post-harvest year (2002) or in the 23 m, partial harvest, or 23 m treatment groups.

Macroinvertebrates

We observed 89 different macroinvertebrate taxa in our study streams in the second post-harvest year (2003). Most samples (from both harvest and upstream stations) were dominated by chironomids (31%–67%), resulting in low diversity as scored by Simpson's diversity index (scores 0.7–0.9) and Shannon–Wiener index (scores 0.9–1.2) (Appendix B). The most common functional feeding groups in all samples (from both harvest and upstream stations) were shredders (19%–61%) and gatherers (14%–49%). Algal feeders (scrapers) were uncommon (1%–6%) in all treatments (Appendix

Table 4. Average differences in pH, specific conductivity, dissolved oxygen, and turbidity measurements between harvest and upstream (unharvested) stations in the pre-harvest and three post-harvest years.

Treatment	Pre-harvest mean (SE)	Post-harvest year 1 mean (SE)	Post-harvest year 2 mean (SE)	Post-harvest year 3 mean (SE)
pH				
0 m	0.10 (0.12)	0.11 (0.11)	0.16 (0.09)	0.13 (0.14)
11 m	0.07 (0.15)	0.02 (0.17)	0.08 (0.19)	0.15 (0.15)
23 m	0.12 (0.10)	0.12 (0.15)	0.11 (0.12)	0.06 (0.12)
Partial harvest	0.19 (0.16)	0.20 (0.16)	0.30 (0.15)	0.18 (0.13)
Control	7.0×10^{-04} (0.02)	0.06 (0.02)	0.06 (0.03)	–0.03 (0.04)
Conductivity (µS·cm^{-1})				
0 m	1.2 (0.2)	0.9 (0.7)	1.6 (0.5)	1.7 (0.4)
11 m	–2.0 (1.9)	–2.2 (2.5)	–0.8 (2.0)	–1.4 (1.9)
23 m	0.1 (0.9)	0.7 (1.0)	1.3 (0.9)	0.3 (1.3)
Partial harvest	0.4 (0.5)	0.7 (0.7)	0.5 (0.5)	0.5 (0.3)
Control	0.0 (0.3)	0.1 (0.3)	0.1 (0.2)	–0.4 (0.9)
Dissolved oxygen (mg·L^{-1})				
0 m	0.47(0.51)	–0.15 (0.21)	–0.04 (0.06)	–0.07 (0.12)
11 m	0.52 (0.61)	0.11 (0.32)	0.24 (0.36)	0.53 (0.32)
23 m	0.47 (0.25)	0.27 (0.07)	0.04 (0.21)	0.13 (0.22)
Partial harvest	0.24 (0.05)	0.31 (0.07)	0.13 (0.12)	0.31 (0.11)
Control	0.01 (0.11)	0.02 (0.15)	–0.01 (0.23)	–0.07 (0.31)
Turbidity (NTU)				
0 m	0.050 (0.09)	–0.100 (0.30)	0.060 (0.06)	0.240 (0.20)
11 m	0.040 (0.06)	0.150 (0.27)	0.270 (0.27)	0.270 (0.22)
23 m	0.030 (0.09)	–0.020 (0.10)	–0.020 (0.10)	–0.009 (0.07)
Partial harvest	0.060 (0.07)	0.010 (0.02)	0.009 (0.02)	0.070 (0.12)
Control	0.002 (0.04)	–0.040 (0.02)	4.0×10^{-04} (0.01)	–0.130 (0.05)

Note: Differences between harvest and upstream (unharvested) stations were calculated for each stream and averaged by treatment group. Positive numbers indicate larger values at the downstream station compared with the upstream station, while negative numbers indicate a smaller value at the downstream stations than at the upstream station. Statistical analysis (PROC MIXED) showed no significant differences ($\alpha < 0.05$) between treatment groups or years. Each treatment group consists of three streams.

Table 5. Differences in chlorophyll *a* and SRP concentrations between harvest and upstream stations in the pre-harvest and two post-harvest years.

Treatment	*n*	Pre-harvest mean (SE)	Post-harvest year 1 mean (SE)	Post-harvest year 2 mean (SE)
Chlorophyll-a (mg·m^{-2})				
0 m	3	–0.20 (0.46)	1.34 (2.29)	**15.85** (6.74)
11 m	3	0.68 (0.17)	4.95 (2.38)	7.43 (1.34)
23 m	2–3*	0.59 (1.17)	–1.55 (1.62)	0.61 (0.12)
Partial harvest	2–3[†]	0.15 (0.31)	1.89 (1.36)	2.04 (0.99)
Control	2–3[‡]	–0.25 (0.77)	1.15 (1.65)	–5.11 (4.98)
SRP (ppm)				
0 m	3	–0.001 (0.000)	–0.002 (0.001)	–0.002 (0.002)
11 m	3	0.000 (0.000)	0.001 (0.001)	0.000 (0.000)
23 m	2–3*	–0.003 (0.004)	–0.003 (0.006)	–0.004 (0.007)
Partial harvest	2–3[†]	0.000 (0.000)	0.000 (0.000)	0.000 (0.001)
Control	2–3[‡]	0.000 (0.000)	0.000 (0.000)	0.001 (0.001)

Note: Differences between harvest and upstream (unharvested) sampling stations were calculated for each stream and averaged by treatment group. Negative numbers indicate lower concentrations at the downstream stations and positive numbers indicate higher concentrations of at the downstream stations compared with the upstream stations. Treatment means with boldface type indicate significant differences from pre-harvest values within a treatment group based on Bonferroni-adjusted multiple *t* tests (Dunn 1961).

*Pre-harvest: $n = 2$, post-harvest year 1: $n = 3$, post-harvest year 2: $n = 2$.

[†] Pre-harvest: $n = 3$, Post-harvest year 1: $n = 3$, Post year 2: $n = 2$.

[‡] Pre-harvest: $n = 3$, post-harvest year 1: $n = 2$, post-harvest year 2: $n = 2$.

Table 6. Difference (mean (SE)) between harvest and upstream (unharvested) stations for macroinvertebrate diversity metrics in the second post-harvest year.

	0 m ($n = 3$)	11 m ($n = 2$)	23 m ($n = 3$)	Partial harvest ($n = 3$)	Control ($n = 2$)	p
Corrected abundance	–240 (724)	–115 (340)	353 (523)	67 (138)	289 (107)	0.564
Species richness	2 (6)	9 (12)	1 (23)	7 (4)	6 (4)	0.948
Shannon–Wiener index (log 10)	0.07 (0.11)	0.13 (0.13)	0.07 (0.61)	0.09 (0.24)	–0.20 (0.35)	0.885
Simpson's index	0.02 (0.03)	0.02 (0.03)	0.07 (0.21)	0.08 (0.15)	–0.18 (0.27)	0.489

Note: Differences between harvest and upstream (unharvested) stations were calculated for each stream and averaged by treatment group. Positive numbers indicate larger values at the downstream station compared with the upstream station, while negative numbers indicate a smaller value at the downstream stations than at the upstream station. Statistical analysis (PROC MIXED) was used to test for significant differences among treatment groups.

Table 7. Significant macroinvertebrate indicator species and the relative abundance (%) by treatment group.

	0 m	11 m	23 m	Partial harvest	Unharvested	p
Diptera *Cricotopus* sp.	98	0	0	1	1	0.002
Diptera *Psectrocladius* sp.	98	0	0	0	2	0.037
n	3	2	3	3	15	

B). Differences in corrected abundance ($p = 0.564$), species richness ($p = 0.948$), and diversity indices (Shannon–Wiener index: $p = 0.885$; Simpson's diversity index: $p = 0.489$) between stations were not significant among treatment groups (Table 6).

Indicator species analysis found Diptera *Cricotopus* (indicator value of 98%, $p = 0.002$) and Diptera *Psectrocladius* (indicator value of 65%, $p = 0.037$) to be significant indicator taxa for 0 m treatment group (Table 7, Monte Carlo randomization with 1000 permutations). Both *Cricotopus* and *Psectrocladius* are within the subfamily Orthocladiinae. No other taxa were found to be significant indicators of treatment groups ($p > 0.05$).

Periphyton species

In the pre-treatment year, the dominant periphyton species in all sampled streams was *Achnanthes minutissimum* at both harvest and upstream stations and comprised between 24.6% and 56.6% of the samples (Table 8). In the second year following the harvest in the 0 and 11 m treatment groups, *A. minutissimum* remained the dominant algal species despite significant increases in chlorophyll *a* in the 0 m treatment group and substantial, although nonsignificant, increases in the 11 m treatment group (Table 8).

Discussion

Water quality

Following timber harvesting, stream pH, conductivity, and dissolved oxygen levels were within the range of small, mature-forest watersheds in New England (pH = 3.5–7.8 (Hornbeck et al. 1997), conductivity = 0.019–0.038 $mS \cdot cm^{-1}$ (Noel et al. 1986), and dissolved oxygen = 5–12 $mg \cdot L^{-1}$ (Binkley and Brown 1993; Brown and Binkley 1994)). No significant changes in conductivity, dissolved oxygen, or pH were associated with buffer treatment. Our sampling design may have missed short changes in water quality associated with snowmelt and large rain events but water chemistry at base-flow conditions did not change. Changes in conductivity and dissolved oxygen concentrations are not commonly associated with timber harvests in high-gradient streams (Martin et al. 1984; Binkley and Brown 1993). Changes in pH following timber harvest have been attributed to soil characteristics at individual sites (White and Krause 1993; Stafford et al. 1996) and not to harvest treatments (Likens et al. 1970; Martin et al. 1984). Our results are consistent with others studies showing no changes in these water chemistry parameters following timber harvest (Noel et al. 1986 (conductivity); Binkley and Brown 1993 (dissolved oxygen); Hornbeck et al. 1986 (pH)).

No significant increases in turbidity were observed in any treatment group, including streams without a buffer. Average turbidity measurements remained low (<0.5 NTU) in all treatment groups. This finding corresponds to other studies that found nonsignificant increases in turbidity following timber harvesting (Aubertin and Patric 1974; Hornbeck et al. 1987; Brown and Binkley 1994). We did not sample turbidity continuously and therefore could have missed short, episodic increases in turbidity after rain events. However, the presence of Simuliidae within the harvest zone of streams in the 0 and 11 m treatment groups (Appendix B) suggests that sediment additions did not occur as a result of the harvest. Simuliidae are very sensitive to fine sediment because the apparatus they use to filter food particles from the water column can easily be clogged (Shaw and Richardson 2001). Simuliidae are found in streams containing few fine particles (Somers et al. 1998) and therefore indicate that even the most severe treatments had good water clarity.

We attribute the lack of post-harvest changes in turbidity to successful implementation of BMPs, which resulted in few occurrences of exposed mineral soil within 8 m of the stream channel. Application of BMPs can dramatically reduce soil erosion and delivery to water bodies (Maine Forest Service 2004). Forested landscapes in the Northeast are not prone to erosion because the soils are well drained and have high infiltration capacities (Hornbeck and Kochenderfer 2000). However, minimal or inadequate application of BMPs can result in major soil movement and delivery to water bodies (Maine Forest Service 2005).

Table 8. Dominant periphyton species and relative abundance (%) at harvest and upstream (unharvested) stations in the pre-harvest and two post-harvest years.

Treatment	Year	Downstream station	%	Upstream station	%
0 m	Pre-harvest	*Achnanthes minutissimum*	29.2	*Achnanthes minutissimum*	41.0
0 m	Post-harvest year 1	*Fragilaria capucina*	46.9	*Achnanthes minutissimum*	17.7
0 m	Post-harvest year 2	*Achnanthes minutissimum*	44.2	*Fragilaria capucina*	20.7
11 m	Pre-harvest	*Achnanthes minutissimum*	56.6	*Achnanthes minutissimum*	28.4
11 m	Post-harvest year 1	*Achnanthes minutissimum*	66.0	*Achnanthes minutissimum*	69.7
11 m	Post-harvest year 2	*Achnanthes minutissimum*	44.8	*Achnanthes minutissimum*	56.1
23 m	Pre-harvest	*Achnanthes minutissimum*	48.5	*Achnanthes minutissimum*	24.6
23 m	Post-harvest year 1	*Oedogonium* sp.	35.3	*Botryococcus sudeticus*	46.5
23 m	Post-harvest year 2	*Audouinella* sp.	30.3	*Oscillatoria formosa*	35.0
Partial harvest	Pre-harvest	*Achnanthes minutissimum*	27.8	*Achnanthes minutissimum*	35.0
Partial harvest	Post-harvest year 1	*Achnanthes minutissimum*	33.4	*Achnanthes minutissimum*	43.7
Partial harvest	Post-harvest year 2	*Achnanthes minutissimum*	36.1	*Achnanthes minutissimum*	28.4

Chlorophyll *a* and SRP

Significant increases in chlorophyll *a* in the 0 m treatment group occurred in the second year following the harvest after the stream channel had been exposed to post-harvest conditions for a year. In the first post-harvest year, sampling occurred in June, before long-term exposure to post-harvest conditions. In the 0 m treatment group, canopy cover was reduced by 59% and stream temperature increased significantly following the harvest (Wilkerson et al. 2006). Primary productivity, and thus concentrations of chlorophyll *a*, are controlled by solar radiation (Kiffney et al. 2003) and water temperature (Sponseller et al. 2001); therefore, it is not surprising to find increases in chlorophyll *a* in these streams. Other studies have observed greater primary productivity in unbuffered streams and attributed the increases to increased solar radiation and stream temperatures (Noel et al. 1986; Kiffney et al. 2003). In the 11 m treatment group, we observed substantial, although nonsignificant, increases in chlorophyll *a* in the second post-harvest year. This increase occurred with a small (3%–8%) reduction in canopy. Previous studies have attributed increases in chlorophyll *a* in narrow or thinned buffers to lateral transmission through sides of the buffers (Brosofske et al. 1997; Kiffney et al. 2003).

Phosphorus is one of the most critical nutrients for autotrophic production and is often the limiting nutrient for the growth of periphyton (Allan 1995; Bernhardt and Likens 2004). Low nutrient levels (SRP concentrations) in our streams indicate either low availability of nutrients or a rapid utilization of available nutrients (Dodds 2003). Biological uptake of phosphorus in streams with increased algal growth (0 m treatment group) could have masked any post-harvest increases in SRP loads.

Periphyton and macroinvertebrate assemblages

Periphyton and macroinvertebrate assemblages in all treatment groups were dominated by taxa adapted to frequent physical disturbance. Appalachian headwater streams have large variability in seasonal flow and are frequently disturbed by floods, drought, and seasonal channel drying (Griffith and Perry 1993; Angradi 1997; Chadwick and Huryn 2007). Biota living in headwater streams must be equipped (physiologically and behaviorally) to tolerate harsh conditions (Griffith and Perry 1993; Angradi et al. 2001; Danehy et al. 2007). In these streams, we observed frequent small rain events and periodic large storms over the course of the study and reductions in surface flow during portions of the summer (Wilkerson et al. 2006). Headwater streams have small storage capacities, and relatively small rain events can substantially increase stream flow in headwater channels (Gomi et al. 2002). The small storage capacities and drainage areas of headwater streams capture less recharge, making headwater streams more prone to drying than larger streams (McMahon and Finlayson 2003; Rivenbark and Jackson 2004; Svec et al. 2005). The frequent changes in stream flow and low summer flows contribute to a frequently disturbed environment.

The dominance of *A. minutissimum* in the majority of treatment groups both before and after the harvest reflects the frequent physical disturbance in our study streams (Biggs et al. 1998; Stevenson and Bahls 1999). *Achnanthes minutissimum* is used as an indicator of physical disturbance by the US Environmental Protection Agency (Stevenson and Bahls 1999) because it quickly colonizes following flooding and scouring events (Biggs et al. 1998; Stevenson and Bahls 1999; Biggs and Kilroy 2000) but is replaced by other species in more stable conditions (Biggs and Kilroy 2000). *Achnanthes minutissimum* is a prostrate form of periphyton and is more resilient to shallow water and low flows than filamentous or stalked forms of periphyton (Danehy et al. 2007; Richardson and Danehy 2007).

The macroinvertebrate assemblages in all treatment groups were dominated by chironomids at both harvest and upstream (control) sampling stations. Chironomidae are widely distributed across many types of aquatic habitat (Huryn and Wallace 2000) and adapted to live in frequently disturbed habitats (Entrekin et al. 2007). Their ability to feed on a wide variety of food sources, high rates of colonization and production (Berg and Hellenthal 1992; Entrekin et al. 2007), and utilization of patchy, ephemeral food resources (Palmer et al. 2000) make chironomids well suited to live in these small headwater streams. The high disturbance in stream flows may strongly influence the macroinvertebrate community by eliminating sensitive and highly specialized species before they can become established.

Harvest-induced changes to macroinvertebrate assemblages were limited to the 0 m treatment group and linked to increased levels of periphyton within the harvest zone of these unbuffered streams. *Cricotopus* and *Psectrocladius* showed differential occurrences within the harvest zone of the 0 m treatment group. *Cricotopus* and *Psectrocladius* are Orthocladiinae chironomids that preferentially feed on algae (Bourassa and Cattaneo 2000; Entrekin et al. 2007). The increases in *Cricotopus* and *Psectrocladius* within the harvest zone may indicate that these organisms exploited the increase levels of algae and were able to tolerate a reduction (–59%) in overhead shade and increased (+1.4–4.4 °C) water temperature.

Periphyton and macroinvertebrate communities in all treatment groups were dominated by *A. minutissimum* and chironomids, taxa that are adapted to frequently disturbed environments. These small headwater streams experienced a high degree of natural variability due to frequent high-flow events and interruption of surface flow. Harvest-induced changes in biological assemblages were limited to streams harvested without a buffer. No large shifts in functional feeding groups occurred but a few algal feeding macroinvertebrates (e.g., *Cricotopus* and *Psectrocladius*) exploited increases in chlorophyll *a* in streams that were harvested without a riparian buffer. The minimal logging impacts observed on aquatic assemblages in these headwater streams may be due to no observed changes in water quality, the small (≤40%) proportion of watershed harvested, and (or) the resilient nature of these communities in low-order, naturally disturbed streams.

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Appendix A

Appendix A appears on the following page.

Table A1. Average turbidity, dissolved oxygen, pH, specific conductivity, chlorophyll *a*, and SRP of study streams in western Maine, USA.

	n	Pre-harvest	Post-harvest year 1	Post-harvest year 2	Post-harvest year 3
Turbidity (NTU)					
0 m	3	0.11 (0.09)	0.21 (0.16)	0.11 (0.09)	0.39 (0.21)
11 m	3	0.09 (0.08)	0.44 (0.18)	0.30 (0.28)	0.40 (0.22)
23 m	3	0.30 (0.12)	0.17 (0.09)	0.14 (0.07)	0.26 (0.09)
Partial harvest	3	0.18 (0.12)	0.07 (0.03)	0.05 (0.02)	0.36 (0.10)
Control	3	0.05 (0.04)	0.08 (0.04)	0.04 (0.03)	0.27 (0.10)
Dissolved oxygen (mg·L^{-1})					
0 m	3	9.69 (0.13)	9.90 (0.18)	9.87 (0.04)	10.11 (0.12)
11 m	3	9.56 (0.35)	9.91 (0.03)	9.64 (0.08)	10.12 (0.17)
23 m	3	10.39 (0.60)	10.91 (0.35)	10.70 (0.52)	10.76 (0.44)
Partial harvest	3	9.86 (0.06)	10.51 (0.28)	10.37 (0.10)	10.75 (0.22)
Control	3	9.61 (0.26)	10.29 (0.50)	10.17 (0.45)	10.07 (0.17)
pH					
0 m	3	6.48 (0.18)	5.98 (0.15)	6.37 (0.23)	6.30 (0.10)
11 m	3	6.61 (0.22)	6.11 (0.17)	6.37 (0.22)	6.37 (0.23)
23 m	3	6.62 (0.04)	6.17 (0.13)	6.48 (0.13)	6.38 (0.08)
Partial harvest	3	6.60 (0.06)	6.21 (0.07)	6.45 (0.07)	6.38 (0.05)
Control	3	5.76 (0.52)	5.49 (0.48)	5.63 (0.45)	5.45 (0.45)
Specific conductivity (μS·cm^{-1})					
0 m	3	20.0 (1.8)	21.0 (1.9)	19.0 (1.9)	20.8 (1.4)
11 m	3	24.0 (3.7)	22.7 (3.3)	22.4 (2.9)	23.3 (3.3)
23 m	3	25.9 (2.4)	24.3 (3.5)	24.3 (2.8)	25.6 (2.3)
Partial harvest	3	22.6 (1.6)	22.9 (0.5)	21.0 (0.3)	21.9 (0.6)
Control	3	17.6 (2.5)	17.6 (2.1)	16.7 (2.0)	15.7 (1.2)
Chlorophyll *a* (mg·m^{-2})					
0 m	3	1.57 (0.53)	4.83 (2.46)	22.57 (7.18)	na
11 m	3	1.88 (0.19)	9.65 (3.73)	9.88 (2.21)	na
23 m	2–3*	2.67 (0.97)	7.59 (1.97)	6.83 (1.52)	na
Partial harvest	2–3†	1.52 (0.58)	6.52 (3.03)	4.33 (1.06)	na
Control	2–3‡	2.66 (0.70)	5.38 (0.89)	5.76 (0.54)	na
SRP (ppm)					
0 m	3	0.003 (0.001)	0.001 (0.000)	0.002 (0.001)	na
11 m	3	0.002 (0.000)	0.001 (0.000)	0.002 (0.000)	na
23 m	2–3*	0.007 (0.002)	0.004 (0.001)	0.006 (0.001)	na
Partial harvest	2–3†	0.002 (0.001)	0.002 (0.000)	0.003 (0.000)	na
Control	2–3‡	0.002 (0.000)	0.001 (0.000)	0.002 (0.001)	na

Note: Pre-harvest sampling occurred in 2001 before the timber harvest and post-harvest sampling occurred in 2002–2004. na, not available.

*Pre-harvest: *n* = 2, post-harvest year 1: *n* = 3, post-harvest year 2: *n* = 2.

†Pre-harvest: *n* = 3, post-harvest year 1: *n* = 3, post-harvest year 2: *n* = 2.

‡Pre-harvest: *n* = 3, post-harvest year 1: *n* = 2, post-harvest year 2: *n* = 2.

Appendix B

Appendix B appears on the following page.

Table B1. Mean (SE) corrected abundance, diversity metrics, functional feeding groups, and community composition metrics for macroinvertebrate samples of study sites in western Maine, USA.

	0 m (*n* = 3)		11 m (*n* = 2)		23 m (*n* = 3)		Partial harvest (*n* = 3)		Control (*n* = 2)	
	Harvest	Upstream	Harvest	Upstream	Harvest	Upstream	Harvest	Upstream	Harvest	Upstream
Corrected abundance (no. of individuals adjusted for subsampling)										
	393 (156)	633 (305)	454 (275)	569 (515)	705 (269)	352 (40)	652 (408)	585 (486)	795 (306)	506 (383)
Diversity metrics										
Species richness	33 (2)	31 (6)	32 (3)	23 (6)	41 (1)	41 (14)	34 (4)	2 (6)8	33 (10)	28 (8)
Shannon–Wiener (log 10)	1.19 (0.09)	1.12 (0.08)	1.16 (0.08)	1.04 (0.02)	1.28 (0.05)	1.20 (0.33)	1.09 (0.06)	1.00 (0.19)	0.91 (0.31)	1.11 (0.06)
Simpson's index	0.91 (0.02)	0.88 (0.02)	0.9 (0.02)	0.88 (0.01)	0.91 (0.02	0.84 (0.12)	0.86 (0.02)	0.78 (0.10)	0.7 (0.19)	0.88 (0.00)
Functional feeding groups (% of sample)										
Filterer	15 (4)	4 (3)	15 (5)	2 (2)	7 (0)	11 (6)	13 (10)	26 (18)	6 (2)	10 (3)
Gatherer	34 (8)	30 (3)	2 (6)1	41 (22)	45 (9)	49 (15)	22 (5)	14 (4)	22 (15)	23 (7)
Predator	12 (6)	13 (5)	9 (3)	10 (6)	12 (5)	15 (7)	10 (1)	12 (4)	7 (3)	14 (2)
Scraper	4 (2)	3 (3)	2 (2)	6 (5)	1 (0)	2 (1)	4 (2)	4 (2)	2 (2)	6 (6)
Shredder	32 (6)	45 (9)	50 (7)	40 (10)	31 (4)	19 (11)	49 (6)	42 (12)	61 (22)	47 (10)
Piercer	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Unclassified	2 (0)	4 (3)	1 (1)	1 (1)	4 (2)	4 (3)	1 (0)	2 (1)	1 (1)	1 (0)
Community composition metrics (% of sample)										
Coleoptera	0 (0)	0 (0)	2 (2)	2 (0)	1 (1)	2 (1)	0 (0)	1 (1)	0 (0)	0 (0)
Diptera	15 (4)	5 (4)	13 (2)	3 (2)	5 (2)	13 (4)	14 (10)	26 (19)	4 (0)	8 (4)
Simuliidae	12 (5)	4 (4)	12 (2)	2 (2)	4 (2)	9 (6)	13 (9)	7 (5)	3 (1)	25 (19)
Tipulidae	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Diptera chironomid	47 (10)	49 (7)	47 (0)	43 (16)	37 (9)	54 (12)	35 (13)	27 (9)	55 (20)	23 (5)
Chironominae	4 (3)	14 (5)	13 (13)	1 (1)	4 (0)	6 (3)	10 (6)	5 (4)	10 (9	6 (1)
Diamesinae	1 (0)	3 (2)	0 (0)	0 (0)	2 (1)	5 (5)	1 (0)	3 (3)	0 (0)	1 (1)
Orthocladiinae	42 (13)	31 (5)	34 (12)	39 (11)	31 (8)	42 (10)	24 (8)	13 (5)	44 (29)	20 (9)
Podonominae	1 (0)	1 (0)	0 (0)	2 (2)	1 (0)	1 (0)	7 (0)	1 (0)	0 (0)	2 (1)
Ephemeroptera	10 (5)	8 (3)	3 (3)	7 (6)	17 (9)	5 (2)	7 (0)	4 (2)	13 (13)	19 (17)
Plecoptera	8 (4)	18 (8)	15 (5)	2 (1)	27 (6)	10 (6)	20 (9)	14 (5)	19 (9)	31 (0)
Leuctridae	4 (2)	5 (3)	0 (0)	0 (0)	9 (3)	4 (4)	2 (2)	2 (0)	2 (1)	3 (0)
Nemouridae	3 (2)	12 (7)	10 (8)	1 (1)	12 (6)	3 (2)	15 (7)	10 (5)	16 (6)	23 (3)
Trichoptera	11 (2)	16 (6)	20 (4)	29 (12)	11 (4)	11 (5)	19 (8)	22 (10)	6 (0)	13 (2)

Note: Samples were collected from 13 study streams 2 years after timber harvest (2003) from within the harvest zone (harvest sample) and upstream of the harvest zone (upstream sample).