

APPLIED ISSUES

# Influences of logging history and riparian forest characteristics on macroinvertebrates and brook trout (*Salvelinus fontinalis*) in headwater streams (New Hampshire, U.S.A.)

KEITH H. NISLOW\* AND WINSOR H. LOWE†

\*USDA Forest Service Northeastern Research Station, UMASS, Amherst, MA, U.S.A.

†Institute of Ecosystem Studies, Millbrook, NY, U.S.A.

## SUMMARY

1. Logging can strongly affect stream macroinvertebrate communities, but the direction and magnitude of these effects and their implications for trout abundance are frequently region-specific and difficult to predict.
2. In first-order streams in northern New England (U.S.A.) representing a chronosequence of logging history (<2 to >80 years since logging), we measured riparian forest conditions, stream macroinvertebrate community characteristics and brook trout (*Salvelinus fontinalis*) abundance. Principal component analysis was used to collapse forest data into two independent variables representing variation in logging history, riparian forest structure and canopy cover. We used these data to test whether logging history and associated forest conditions were significant predictors of macroinvertebrate abundance and functional feeding group composition, and whether brook trout abundance was related to logging-associated variation in invertebrate communities.
3. Catchments with high PC1 scores (recently logged, high-density stands with low mean tree diameter) and low PC2 scores (low canopy cover) had significantly higher total macroinvertebrate abundance, particularly with respect to chironomid larvae (low PC2 scores) and invertebrates in the grazer functional feeding group (high PC1 scores). In contrast, proportional representation of macroinvertebrates in the shredder functional feeding group increased with time since logging and canopy cover (high PC2 scores). Brook trout density and biomass was significantly greater in young, recently logged stands (high PC1 scores) and was positively related to overall macroinvertebrate abundance. In addition, three variables – trout density, invertebrate abundance and shredder abundance – successfully discriminated between streams that were less-impacted versus more-impacted by forestry.
4. These results indicate that timber harvest in northern New England headwater streams may shift shredder-dominated macroinvertebrate communities supporting low trout abundance to a grazer/chironomid-dominated macroinvertebrate community supporting higher trout abundance. However, while local effects on brook trout abundance may be positive, these benefits may be outweighed by negative effects of brook trout on co-occurring species, as well as impairment of habitat quality

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Correspondence: Keith H. Nislow, USDA Forest Service Northeastern Research Station, UMASS, Amherst, MA 01003, U.S.A.  
E-mail: knislow@fs.fed.us

Present address: Winsor H. Lowe, Division of Biological Sciences, The University of Montana, Missoula, MT, U.S.A.

downstream. Research testing the generality of these patterns will improve understanding of how aquatic ecosystems respond to anthropogenic and natural trajectories of forest change.

*Keywords:* brook trout, disturbance, food webs, forest succession, *Salvelinus fontinalis*, small watersheds, timber harvest

## Introduction

The New England region of the U.S.A. has a complex land use history involving multiple anthropogenic stresses to stream ecosystems. Chief among these is intensive timber harvest, both historical (Foster, 1992) and present-day (Miller, Bryant & Birnie, 1998). A large body of previous research has provided general agreement on the suite of physical effects resulting from logging practices (e.g. Garman & Moring, 1991; Waters, 1995; Hartman, Scrivener & Miles, 1996), all of which are generally applicable to New England streams. Logging may strongly influence the distribution and abundance of stream macroinvertebrates, critical links in headwater stream food webs (e.g. Stone & Wallace, 1998; Williams *et al.*, 2002). However, the response of invertebrate communities to physical changes associated with logging is difficult to predict, and studies from different regions have often shown contradictory results. Increased sedimentation and embeddedness has been shown to decrease overall invertebrate abundance and diversity in some studies (Murphy, Hawkins & Anderson, 1981; Harding *et al.*, 1998), while in others, increased light penetration and nutrient availability have yielded higher standing stocks of invertebrate biomass in logged catchments (Gurtz & Wallace, 1984; Anderson, 1992; Kiffney, Richardson & Bull, 2003).

Extending up the food web, the relationship between logging-associated changes in invertebrate abundance, the trophic structure of the invertebrate community and fish abundance is also complex. There is some evidence that resident trout are food-limited in headwater streams (Cada, Loar & Sale, 1987; Boss & Richardson, 2002) and that logging-associated increases in macroinvertebrate abundance yield higher individual growth rates (Wilzbach, 1985). However, under some sets of conditions logging-associated habitat alteration can counteract these positives and reduce trout production (Bisson *et al.*, 1992; Hartman

*et al.*, 1996; Flaspohler *et al.*, 2002), particularly when fine sediment is introduced into the streambed (Suttle *et al.*, 2004).

A major part of the variation among studies in the response of macroinvertebrates to logging is likely associated with regional differences in logging practices, forest dynamics and environmental characteristics. For example, logging in the New England region is generally associated with small-scale selection or group cuts (Miller *et al.*, 1998; Lowe & Bolger, 2002; Kittredge, Finley & Foster, 2003) as opposed to the extensive even-aged management characteristic of Pacific Northwest forests (Anderson, 1992; Bisson *et al.*, 1992; Grialou, West & Wilkins, 2000). Similarly, natural regeneration of logged stands is rapid in New England, and gentler slopes likely reduce the probability of sedimentation and catastrophic debris flows (Bormann & Likens, 1979). In this study, we sampled forest conditions, macroinvertebrates, and brook trout (*Salvelinus fontinalis* Mitchill) abundance in headwater streams located throughout New Hampshire, U.S.A., that encompassed a chronosequence of logging history. Our goal was to assess the implications of this aspect of landscape change on macroinvertebrate communities and higher trophic levels in headwater streams in order to better inform conservation and management of these systems. Specifically, we provided an assessment of the potential consequences of variation in forest age, a forest attribute that is strongly influenced by both forestry practices and natural trajectories of change in this largely reforested region.

## Methods

### *Study sites*

This study was conducted in first-order streams of known logging history in New Hampshire, U.S.A., in and adjacent to the White Mountain National Forest. Invertebrates were sampled in 22 streams, trout were

sampled in 16 streams and forest structure in 15 streams. All streams were <1 km in total length, <2 km<sup>2</sup> in drainage area and have not been stocked with brook trout for at least several decades. Bankfull channel widths were <5 m. The general terrain of these drainages was moderately sloped (2–4% slopes). Forests were a combination of northern hardwoods [primary species including *Acer saccharum* (Marsh), *Betula alleghaniensis* (Britton), *Fagus grandifolia* (Erhart), *Betula papyrifera* (Marsh), and *Populus tremuloides* (Michx) and spruce-fir (*Picea rubens* (Sargeant) and *Abies balsamea* (Linnaeus)] cover types (see Lowe & Bolger, 2002; Nislow & Lowe, 2003 for more details on the study streams). Such small first-order streams have two important advantages for our design: (i) they can be considered independent replicates for statistical analysis and (ii) it is reasonable to assume that due to the small size of these catchments, within-catchment spatial variation in logging intensity was minimal and that riparian buffer strips were not purposefully left. This assumption was corroborated by interviews with district and private foresters and supplemented by site inspections. We established 100 m long study sections in each stream, starting 25 m upstream of the confluence of the first-order study stream with a larger stream.

#### *Forest surveys*

Forest and logging history assessments followed the methods of Lowe & Bolger (2002) and Lowe, Nislow & Likens (2005). Our measure of logging history in each of the study drainages was the number of years since the last harvest. To assess riparian forest structure and composition, we set six, 50 m long by 1 m wide belt transects perpendicular to the stream channel at random locations along each study section. Three transects were placed on each side of the stream. We then counted and measured the diameter at breast height (DBH, cm) of all trees with DBH ≥ 3.0 cm within the transects. These data were used to calculate mean tree density (stems 500 m<sup>2</sup> transect<sup>-1</sup>) and mean tree DBH (calculated using mean DBH values from each of the six transects). Using a spherical densiometer we measured proportion canopy coverage over the stream (i.e. standing in the middle of the channel) at six locations randomly selected along the length of the 100-m long study section and used these data to calculate mean

canopy cover. We also categorised 16 streams as less-impacted or more-impacted by forestry based on the previously discussed measurements, interviews with forestry personnel and instream habitat conditions, particularly embeddedness (the extent to which large substrate elements were embedded in fine sediment), which was significantly higher in recently logged streams (Lowe & Bolger, 2002; Nislow & Lowe, 2003; Lowe, Nislow & Bolger, 2004). Six streams were classified into the more-impacted category, and ten streams into the less-impacted category.

#### *Invertebrate surveys*

We collected benthic invertebrates from study streams in the last week of June 2001. Invertebrates were sampled at three stations located randomly within the upper, middle and lower reaches of the study sections. At each station, six arbitrarily placed Surber samples were collected (sample area = 0.09 m<sup>2</sup>, net mesh size = 350 µm) and then composited into a single sample of 0.54 m<sup>2</sup> of the stream bottom, resulting in three replicates per stream. Invertebrates were preserved in 95% ethanol and transported to the laboratory, where all individuals in each sample were identified to the family taxonomic level and assigned to functional feeding group membership according to Merritt & Cummins (1996).

#### *Fish sampling*

We sampled brook trout within the 100 m long study sections during a 1-week period in late August 2000. Electrofishing surveys involved three-pass removals using a Smith-Root BP-12 backpack electroshocker set to 500 V DC. Block nets were used to prevent movement in and out of the study section during electrofishing. Upon capture, each fish was anaesthetised using MS-222, weighed and measured and then returned to the stream. A modified Zippin maximum likelihood method was used to estimate population size (Carle & Strub, 1978). Mortalities were low (three fish total) and catchability estimates were high (77–98%) over the course of the study.

#### *Data analysis*

We used a combination of principal component analysis (PCA) and discriminant function analysis

(DFA), along with multiple and simple linear regression to test whether variation in years since logging and riparian forest conditions was significantly associated with variation in macroinvertebrate abundance and functional feeding group structure among the study streams and with variation in brook trout abundance. These multivariate techniques were applied to the 14 streams where forest structure, invertebrate and trout data were all available. PCA was used on the forest variables (years since logging, stem density, mean DBH and canopy cover) to extract independent axes of variation that could then be used as independent predictor variables in multiple linear regression analyses (Kleinbaum *et al.*, 1998). Multiple regressions (using a backwards-stepwise selection procedure with  $\alpha = 0.15$  to remove) were then used to test for effects of logging history and riparian forest conditions, represented by principal components, on (i) total invertebrate abundance, (ii) abundances and proportional representations of invertebrate functional feeding groups (predators, grazers, collector-gatherers, collector-filterers and shredders) and (iii) brook trout density and biomass. We used DFA (using a backwards-stepwise selection procedure with  $\alpha = 0.15$  to remove) to test whether selected invertebrate and trout variables (trout density, invertebrate abundance, grazer abundance

and shredder abundance) could discriminate between more-impacted and less-impacted streams. We also used simple regression to test the relationship between brook trout density and total invertebrate abundance. All data were tested for normality and appropriately transformed prior to analysis.

## Results

### Forest structure

Forest stands showed considerable variation in all characteristics measured (Table 1). Stem densities and DBH values of stands that had not been recently logged were typical of mid- and late-successional forests in the region. On average, PCA effectively summarised the variation in the four forest-related variables, with the first two components accounting for 80% of the total variation in the dataset (Table 2). PC1 (52.8% of the total variation) was negatively correlated with years since logging and mean DBH, and positively correlated with stem density. Catchments with high PC1 scores were therefore associated with young, dense forest stands. PC2 (27.2% of the total variation) was most strongly positively correlated with canopy cover, and to a lesser degree, with years since logging. Catchments with high PC2 scores

**Table 1** Descriptive statistics for riparian forest conditions, stream invertebrates and fish populations in the study streams. For stream macroinvertebrates, a 'sample' corresponds to a 0.54 m<sup>2</sup> area of streambed (a composite of six 0.09 m<sup>2</sup> Surber samples). 'SE' = standard error.

Variable	Units	Minimum	Maximum	Mean	SE
Riparian forests					
Years since logging	years	2	94	23.92	4.33
Mean diameter at breast height	cm	6.4	17.48	11.1	0.74
Stem density	mean number 500 m <sup>2</sup> transect <sup>-1</sup>	66	134	98.33	6.14
Proportion conifers	proportion	0.11	0.736	0.468	0.046
Proportion canopy cover	proportion	0.83	0.95	0.909	0.007
Stream macroinvertebrates					
Invertebrate family richness	number sample <sup>-1</sup>	8	22	17	0.72
Total invertebrate abundance	individuals sample <sup>-1</sup>	100	1124	493.2	528.6
Grazer abundance	individuals sample <sup>-1</sup>	0	378	61.4	18.42
Shredder abundance	individuals sample <sup>-1</sup>	1	278	90.07	13.58
Collector-filterer abundance	individuals sample <sup>-1</sup>	0	106	31.93	6.2
Collector-gatherer abundance	individuals sample <sup>-1</sup>	0	90	34.27	5.96
Predator abundance	individuals sample <sup>-1</sup>	2	242	63.7	11.85
Chironomid abundance	individuals sample <sup>-1</sup>	32	435	168.7	24.54
Fish populations					
Brook trout abundance	individuals 100 m section <sup>-1</sup>	0	94	32.06	7.49

**Table 2.** Factor loadings for the first two principal components derived from the analysis of forest variables measured in the 15 first-order study streams. Percentage of the total variance explained by each of these principal components is provided in the bottom row.

Factor	PC1	PC2
Years since logging	-0.806	0.381
Mean diameter at breast height	-0.676	-0.593
Stem density	0.878	0.135
Proportion conifers	0.619	-0.645
Proportion canopy cover	0.248	0.757
Percentage of total variance explained	52.8	27.2

were therefore associated with older forest stands that provided a high level of shade to the stream.

#### Macroinvertebrate communities

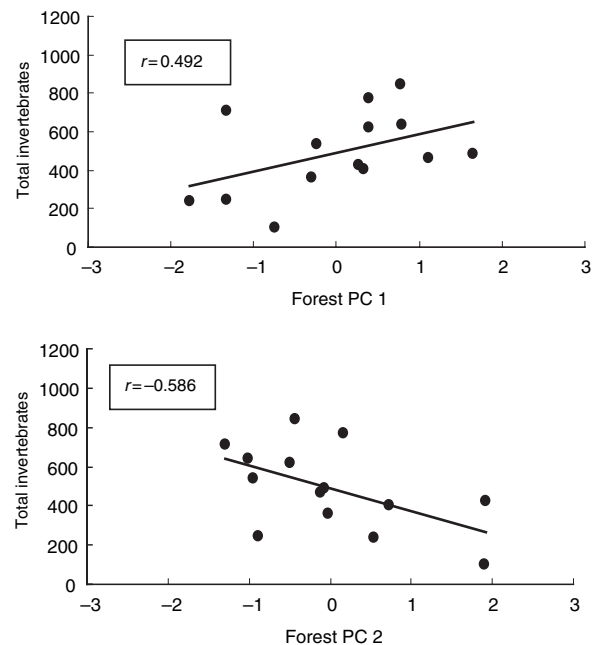
We found a diverse assemblage of macroinvertebrates in the study streams, typical of headwater stream habitats, with invertebrate family richness ranging from 8 to 22 per site (Table 1). Chironomid larvae (which were not assigned to specific functional feeding groups because of feeding diversity within the family) were the most abundant taxon in the samples ( $169 \pm 24.5$  individuals sample<sup>-1</sup>; Table 1), with several other families having strong representation across sites. Abundances were fairly well distributed across functional feeding groups, with shredders and grazers generally most abundant (Table 1). Heptageniid and baetid mayflies, along with elmids beetles were the dominant grazers. Leuctrid and nemourid stoneflies, and lepidostomatid caddisflies were the dominant shredders.

#### Brook trout abundance

Brook trout were found in 12 of 15 streams surveyed, with a total of 498 individuals captured (Table 1). No other fish species were found. The number of trout in the 100 m long study sections ranged from 0 to 94, with fish size ranging from 31 to 180 mm fork length and 0.51 to 63.6 g wet weight. Both age-0 and older fish were present, and based on visual characteristics (fin shape, coloration), we had no indication that any fish were of hatchery origin. A second round of electrofishing on a subset of these sites in August 2002 yielded similar results, indicating that differences among sites were consistent across years.

#### Relationships among forest structure, macroinvertebrates and brook trout

Invertebrate abundance and functional feeding group composition was significantly related to forest structure and forest history. The multiple regression model relating variation in forest PC scores to total invertebrate abundance was significant ( $R^2 = 0.586$ ,  $P = 0.008$ ). Streams draining more recently logged catchments with dense, young forest stands (high PC1 scores) had significantly greater total invertebrate abundance (partial correlation = 0.492,  $P = 0.028$ ). Total invertebrate abundance was negatively associated with PC2, decreasing in older stands with higher canopy cover (partial correlation = -0.586,  $P = 0.012$ ; Fig. 1; Table 3). The positive relationship between PC1 and total invertebrates was largely accounted for by the positive relationship between PC1 (as well as some of the raw variables significantly associated with PC1) and invertebrate grazers (partial correlation = 0.604,  $P = 0.022$ ). The negative relationship between PC2 and total invertebrates was associated with the significant negative relationship with chironomid

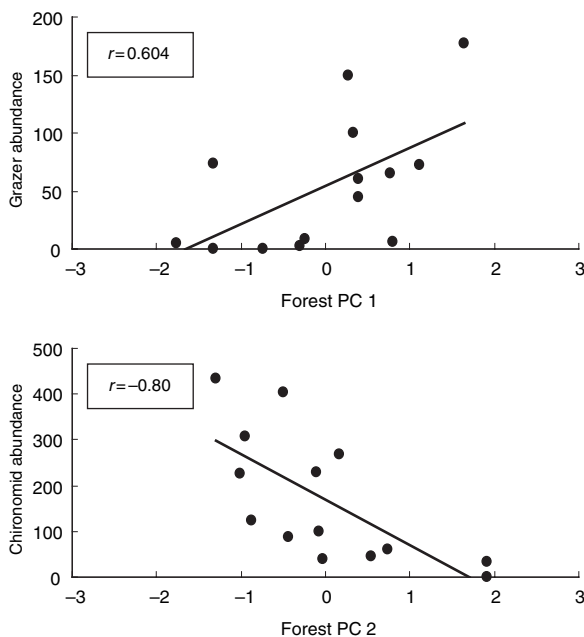


**Fig. 1** Relationship between total invertebrate abundance (mean number sample<sup>-1</sup>) and forest principal components 1 and 2 in 14 study streams. For stream macroinvertebrate data, a 'sample' corresponds to a 0.54 m<sup>2</sup> area of streambed (a composite of six 0.09 m<sup>2</sup> Surber samples).

**Table 3** Correlation matrix for forest, invertebrate and trout variables. Numbers in bold indicate correlation coefficients that are significant at the  $P < 0.05$  level (uncorrected for multiple comparisons).

	Years since logging	Mean DBH	Stem density	Proportion canopy cover
Trout density	<b>-0.673</b>	<b>-0.587</b>	<b>0.713</b>	-0.043
Invertebrate density	<b>-0.701</b>	-0.194	0.462	0.151
Invertebrate richness	<b>-0.541</b>	<b>-0.529</b>	0.489	-0.065
Invertebrate diversity	0.389	-0.307	-0.033	-0.400
Grazer density	-0.441	<b>-0.547</b>	0.244	<b>-0.571</b>
Shredder density	-0.008	-0.181	0.086	-0.119
Collector-Filterer density	-0.185	0.317	-0.335	-0.149
Collector-Gatherer density	-0.364	<b>-0.569</b>	0.477	-0.323
Predator density	-0.195	-0.459	0.356	-0.288
Grazer proportion	-0.347	<b>-0.553</b>	0.184	<b>-0.635</b>
Shredder proportion	<b>0.609</b>	0.014	-0.312	-0.259
Collector-Filterer proportion	0.354	0.426	<b>-0.621</b>	-0.298
Collector-Gatherer proportion	-0.022	-0.472	0.199	-0.219
Predator proportion	0.139	-0.341	0.034	-0.381

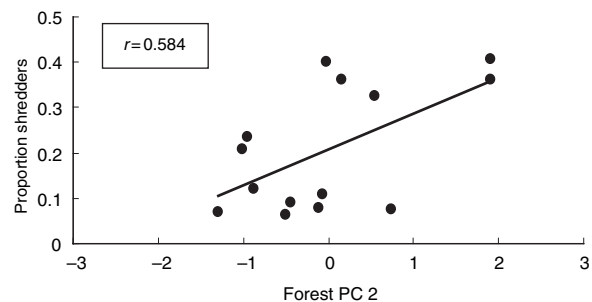
larvae, as low canopy cover, recently logged streams had higher chironomid abundances (partial correlation = 0.80,  $P = 0.001$ ; Fig. 2; Table 3). Abundances of invertebrates in the collector-gatherer, collector-filterer and shredder functional feeding groups were not



**Fig. 2** Relationship between forest principal component 1 and the abundance (mean number sample<sup>-1</sup>) of macroinvertebrates in the grazer functional feeding group (upper panel) and between forest principal component 2 and the abundance of chironomids (lower panel) in 14 study streams. For stream macroinvertebrate data, a 'sample' corresponds to a 0.54 m<sup>2</sup> area of streambed (a composite of six 0.09 m<sup>2</sup> Surber samples).

significantly associated with either PC axis. With respect to functional feeding group composition, the proportional representation of shredders was positively correlated with PC2 (partial correlation = -0.584,  $P = 0.027$ ), increasing with canopy cover and stand age (Fig. 3; Table 3). Proportional representations of the remaining functional feeding groups were not related to either of the forest PC axes. There was also no relationship between invertebrate diversity and either of the forest PC axes.

Brook trout density (number 100 m<sup>-1</sup>) and total biomass (g 100 m<sup>-1</sup>) were significantly related to the forest PC axes in the multiple regression analysis ( $R^2 = 0.609$ ,  $P = 0.002$ ). Similar to total invertebrate abundance, trout density was positively related to PC1 and negatively related to PC2, being greater in streams draining young, dense forest stands (Fig. 4).



**Fig. 3** Relationships between forest principal component 2 and proportional representation of invertebrates in the shredder functional feeding group. For stream macroinvertebrate data, a 'sample' corresponds to a 0.54 m<sup>2</sup> area of streambed (a composite of six 0.09 m<sup>2</sup> Surber samples).

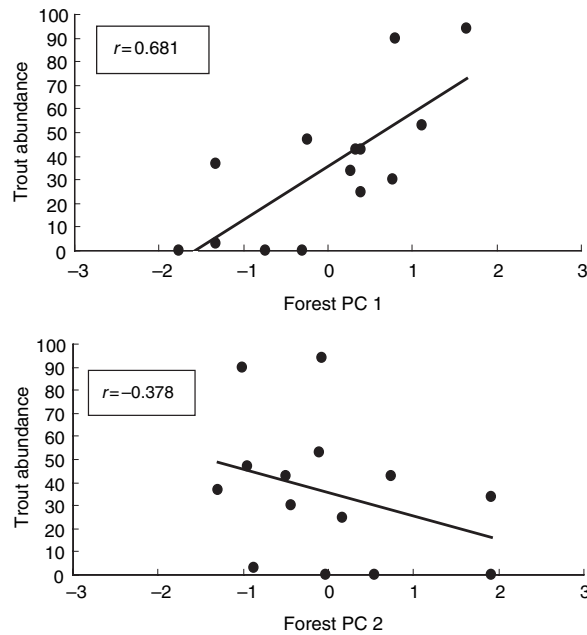


Fig. 4 Relationships between brook trout abundance (number 100 m sample section<sup>-1</sup>) and forest principal components 1 (upper panel) and 2 (lower panel) in 14 study streams.

Trout density ( $r^2 = 0.431$ ,  $P = 0.003$ ) and biomass ( $r^2 = 0.26$ ,  $P = 0.044$ ) were directly and positively related to total invertebrate abundance using simple regression. Neither trout density nor biomass was correlated with abundances or proportional representations of particular invertebrate functional feeding groups, and there was no relationship between mean trout size (either length or mass) and forest PC axes (multiple regression length,  $R^2 = 0.12$ ,  $P = 0.599$ ; mass,  $R^2 = 0.27$ ,  $P = 0.29$ ) or invertebrate abundance (simple regression, length  $r^2 = 0.16$ ,  $P = 0.195$ ; mass,  $r^2 = 0.21$ ,  $P = 0.27$ ).

Discriminant function analysis indicated significant differences between less-impacted and more-impacted streams that were strongly consistent with the results of the other analyses. A significant discriminant function (Wilk's Lambda  $F_{[3,12]} = 8.037$ ;  $P = 0.0033$ ), associated with three variables (trout density, total invertebrate abundance and shredder abundance) successfully classified streams into impacted and non-impacted categories (88% jackknifed classification probabilities). Fish density and invertebrate abundance were greater, and shredder abundance lower in impacted versus non-impacted streams.

## Discussion

We found that logging, an important anthropogenic impact on New England streams, was significantly associated with macroinvertebrate abundance and trophic structure. While logging has been shown to influence macroinvertebrate communities in other regions, responses to logging appear to be very region-specific, and these are some of the first data from New England to address this issue. Our results are particularly relevant given the overall trajectory of forest recovery in the region. Specifically, reforestation, forest succession and changes in forest practices are likely to result in re-establishment of mature and more diverse forests throughout northern New England, and particularly in protected riparian buffer zones. The results of this study also may have general implications for the forested ecosystems of the North Atlantic basin. While currently less forested than New England, policies and practices in northwest Europe have encouraged the restoration of native forests, protection of riparian areas and longer harvest rotations (Broadmeadow & Nisbet, 2004; Nislow, 2005). If this recovery trajectory continues, it is vital for managers to be able to predict and respond to likely changes in aquatic ecosystems.

Consistent with a number of previous studies, we found higher macroinvertebrate abundance in streams that had been recently logged (Bisson & Sedell, 1984; Wilzbach, 1985; Kiffney *et al.*, 2003). Increased light penetration (Hill, Ryon & Schilling, 1995) and increased nutrient availability (Bormann & Likens, 1979; Goodale, Aber & McDowell, 2000; Benfield *et al.*, 2001) in response to forest removal may combine to increase autochthonous primary production and invertebrate grazers (Hawkins, Murphy & Anderson, 1982). Our observation that grazer abundance was higher in more recently logged stands supports this mechanism, and the two groups that were most strongly associated with logging history (grazers and chironomids) have been previously observed to increase in response to manipulations of forest cover (Gurtz & Wallace, 1984; Wilzbach, 1985). Our results conflict, however, with a number of studies indicating negative effects of logging on macroinvertebrate communities and production (Reeves, Everest & Sedell, 1993; Hauer *et al.*, 1999). The resilience of New England upland landscapes to the

small-scale, moderate-intensity logging activities characteristic of this region, compared with large-scale, clear-cut logging in landscapes that are more prone to mass wasting and hillslope failures, is likely an important part of this difference in response to logging history. However, we recognise the inherent limitations of this short-term, correlative study, and underscore the need for further research on these important issues.

These increases in invertebrate abundance appear to have implications for higher trophic levels (i.e. fish). In a previous study (Nislow & Lowe, 2003), we found that brook trout abundance was higher in more recently logged streams. In general, increased fish abundance associated with logging may be because of several factors, including greater foraging success under higher light levels (Wilzbach, Cummins & Hall, 1986) and greater metabolic and foraging efficiency because of elevated stream temperatures (Holtby & Scrivener, 1989). However, our observation of increased macroinvertebrate abundance, particularly of trophic groups that represent important pathways to fish production (e.g. grazers and chironomids; Bilby & Bisson, 1992), is consistent with an increase in prey base as the mechanism underlying our previous results. Food limitation of resident trout in unproductive, soft water, upland streams has been suggested by several studies (Cada *et al.*, 1987; Deegan & Peterson, 1992; Boss & Richardson, 2002), and may be particularly important in small streams during the summer low flows of our sampling period, where invertebrate drift densities and drift flux rates are low (Nislow, Sepulveda & Folt, 2004).

In addition to effects on overall invertebrate abundance, changes in forest structure were associated with differences in functional feeding group composition of invertebrate communities. Because of the lower abundances of other functional feeding groups, the proportional representation of shredders was positively related to years since logging in our study streams, and shredder abundance was significantly greater in less-impacted streams. Dominance of shredders in low-order streams is generally expected in heavily forested catchments (Vannote *et al.*, 1980) and is often attributed to light and nutrient limitation of other trophic groups, combined with large inputs of coarse particulate organic material in the form of leaf litter. Increases in both the absolute and relative abundances of other, non-shredder trophic groups associated with

logging is consistent with the prediction that logging disturbance will shift macroinvertebrate communities to those more characteristic of downstream conditions.

In a broader sense, our results suggest that timber harvest in New England headwater streams may shift shredder-dominated macroinvertebrate communities supporting low brook trout densities to a grazer/chironomid-dominated macroinvertebrate community supporting high brook trout densities. By expanding the total area of habitat suitable for brook trout, these changes may increase overall population abundance, particularly when brook trout are excluded from larger streams by invasive species or unsuitable habitat conditions (e.g. Curry *et al.*, 1997). However, increased sedimentation in response to recent logging, as we have observed in previous studies (Lowe & Bolger, 2002), while outweighed by other factors in headwater reaches, may have negative impacts on trout populations in downstream reaches (e.g. Suttle *et al.*, 2004). Also, by increasing trout densities in headwater streams, logging activities may have negative effects on species that are vulnerable to fish predation. Species and communities that are restricted to fishless habitats have been frequently observed in other regions (e.g. Harvey, 1993; Resetarits, 1997; Bradford *et al.*, 1998). In New England, a similar phenomenon may be occurring with the spring salamander (*Gyrinophilus porphyriticus* Green), which is negatively impacted by the presence of trout (Lowe & Bolger, 2002; Lowe *et al.*, 2004). While spring salamander larvae and adults feed on stream invertebrates (Burton, 1976), adults are also able to leave the stream and forage for terrestrial invertebrates in the riparian zone (Lowe *et al.*, 2005). Therefore, this species may be well-suited for survival in the undisturbed, low-productivity streams indicated by low PC1 scores. In contrast, the higher macroinvertebrate abundances that we observed in disturbed streams may negatively impact salamander populations by creating an in-stream prey base sufficient to support trout populations. Currently, we know little about other species that may be restricted to fishless headwater streams of this region. Further studies assessing extinction and colonisation dynamics of stream species with forest succession and testing the generality of the patterns we observed will contribute significantly to our understanding of how aquatic ecosystems respond to anthropogenic and natural trajectories of forest change in New England and other regions.



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