

Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams

Craig D. Snyder, John A. Young, David P. Lemarié, and David R. Smith

Abstract: We conducted a comparative study in the Delaware Water Gap National Recreation Area to determine the potential long-term impacts of hemlock forest decline on stream benthic macroinvertebrate assemblages. Hemlock forests throughout eastern North America have been declining because of the hemlock woolly adelgid, an exotic insect pest. We found aquatic invertebrate community structure to be strongly correlated with forest composition. Streams draining hemlock forests supported significantly more total taxa than streams draining mixed hardwood forests, and over 8% of the taxa were strongly associated with hemlock. In addition, invertebrate taxa were more evenly distributed (i.e., higher Simpson's evenness values) in hemlock-drained streams. In contrast, the number of rare species and total densities were significantly lower in streams draining hemlock, suggesting that diversity differences observed between forest types were not related to stochastic factors associated with sampling and that streams draining mixed hardwood forests may be more productive. Analysis of stream habitat data indicated that streams draining hemlock forests had more stable thermal and hydrologic regimes. Our findings suggest that hemlock decline may result in long-term changes in headwater ecosystems leading to reductions in both within-stream (i.e., alpha) and park-wide (i.e., gamma) benthic community diversity.

Résumé : Une étude comparative dans le Delaware Water Gap National Recreation Area nous a permis de déterminer l'impact potentiel à long terme du déclin des forêts de pruches sur les communautés de macroinvertébrés des cours d'eau. Le déclin des forêts de pruches dans tout l'est de l'Amérique du Nord est causé par le puceron lanigère de la pruche, un ravageur exotique. La structure des communautés d'invertébrés aquatiques est fortement reliée à la composition de la forêt. Les cours d'eau qui coulent dans des forêts de pruches contiennent significativement plus de taxons que ceux qui sont dans des forêts de bois durs mixtes et plus de 8 % des taxons sont fortement associés à la pruche. De plus, les taxons d'invertébrés sont répartis de façon plus régulière (i.e. des valeurs plus élevées de l'indice d'équitabilité de Simpson) dans les cours d'eau des forêts de pruches. En revanche, les nombres d'espèces rares et les densités totales sont significativement plus bas dans les cours d'eau des forêts de pruches, ce qui laisse croire que les différences de diversité observées entre les divers types forestiers ne sont pas reliées à des facteurs stochastiques dus à l'échantillonnage, mais que les cours d'eau qui irriguent les forêts de bois durs mixtes sont probablement plus productives. Une analyse des données sur l'habitat révèle que les régimes thermiques et hydrologiques des cours d'eau des forêts de pruches sont plus stables. Nos résultats laissent entrevoir que le déclin des pruches amènera probablement des changements à long terme dans les écosystèmes d'amont des bassins hydrographiques qui réduiront la diversité des communautés benthiques, tant à l'échelle des cours d'eau individuels (i.e. la diversité alpha) qu'à celle de l'ensemble du parc (i.e. la diversité gamma).

[Traduit par la Rédaction]

Introduction

Eastern hemlock (*Tsuga canadensis*) forests have declined substantially in the last two decades (McClure 1991). Widespread hemlock defoliation and mortality have largely been attributed to the hemlock woolly adelgid (*Adelges tsugae*),

an exotic insect that is native to the Far East. Hemlock woolly adelgid is rapidly spreading throughout the eastern U.S., and once infected, hemlock stands may suffer complete mortality within 5 years (McClure 1991). Recent studies suggest that hemlock regeneration following infestation is largely absent, and no infested tree or stand has been found to exhibit any sign of recovery (Orwig and Foster 1999). A similar lack of regeneration occurred during the mid-Holocene period when hemlock forests throughout North America went through a period of rapid, pathogen-induced decline (Fuller 1998). During that bottleneck, it took about 2000 years for hemlock to recover from the decline.

The ecological impact of losing this important climax forest species is poorly understood but has the potential for significant disturbance to biotic communities by changing the energy availability, microclimate, and distribution and abundance of habitat. Recent paleoecological studies suggest that

Received 14 February 2001. Accepted 18 December 2001.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 28 February 2002.
J16216

C.D. Snyder,¹ J.A. Young, D.P. Lemarié, and D.R. Smith.
United States Geological Survey, Biological Resources
Division, Leetown Science Center, 1700 Leetown Road,
Kearneysville, WV 25430, U.S.A.

¹Corresponding author (e-mail: craig_snyder@usgs.gov).

the mid-Holocene hemlock decline had long-term consequences on the species composition of forest plant (Fuller 1998) and lake plankton (Boucherle et al. 1985) communities. The importance of hemlock to some terrestrial assemblages is well documented. For example, hemlock has been shown to be important winter habitat for white-tailed deer (*Odocoileus virginianus*) (e.g., Reay et al. 1990) and porcupines (*Erethizon dorsatum*) (Griesemer et al. 1998) and nesting habitat for woodland hawks (Speiser and Bosakowski 1987; Bosakowski et al. 1992). Moreover, the distribution of numerous song birds and small mammal species have been linked to hemlock (Mitchell 1999; Yamasake et al. 1999). In contrast, the influence of hemlock on aquatic assemblages has received little attention, and relatively few studies have evaluated the long-term consequences of changing forest composition on stream communities (but see Molles 1982; Stout et al. 1992).

Aquatic macroinvertebrates are primary consumers of terrestrial leaf litter, and their distribution and production have been shown to correlate with components of the surrounding forests (Ross 1963; Wallace et al. 1999). In turn, aquatic invertebrates represent a significant food source for fish, and their feeding activity modifies the form and rate with which leaf material is processed and exported (Cuffney et al. 1990). Therefore, changes in macroinvertebrate community structure associated with forest disturbances may cascade to other aquatic assemblages and affect important stream processes. Furthermore, because emerging insects represent a significant energy source for birds, spiders, and other terrestrial fauna (Jackson and Fisher 1986), aquatic macroinvertebrate responses may feed back to the terrestrial system as well.

There have been numerous reports of significant changes in headwater stream habitat and aquatic invertebrate community structure associated with forest disturbances. However, most of these studies have been designed to evaluate the responses of stream ecosystems to the relatively short-term changes that take place between the death or removal of existing riparian forests and the maturation of new overstory canopies. Of particular importance during this period is the shift in the stream energy base associated with large changes in the amount and timing of leaf litter and large woody debris entering the stream and altered light, temperature, and hydrologic regimes (Likens et al. 1970). Such changes have been shown to have significant effects on available habitat (Naiman et al. 1988), nutrient dynamics (Webster et al. 1992), channel morphology (Gregory 1992), and ultimately the trophic structure and productivity of aquatic invertebrate assemblages (Wallace and Gurtz 1986). There is no reason to believe that similar short-term changes would not accompany the decline of hemlock forests in Delaware Water Gap National Recreation Area (DEWA). However, considerably less is known about the long-term consequences to headwater stream ecosystems of pest-induced changes in forest composition.

The objective of this study was to compare benthic macroinvertebrate community structure and stream habitat in streams draining hemlock and mixed hardwood forests in DEWA. We limited the study to headwater catchments so that forest-specific effects could be isolated from other confounding factors that are present in larger watersheds. Results should yield information useful in predicting the long-

term consequences of hemlock decline on aquatic invertebrate assemblages. Because hemlock regeneration following hemlock woolly adelgid induced mortality is poor and overstory recruitment is largely limited to mixed hardwood species in affected stands (Fuller 1998; Orwig and Foster 1998), we believe that our predictions reflect realistic assumptions regarding long-term changes in forest composition.

Materials and methods

Study area

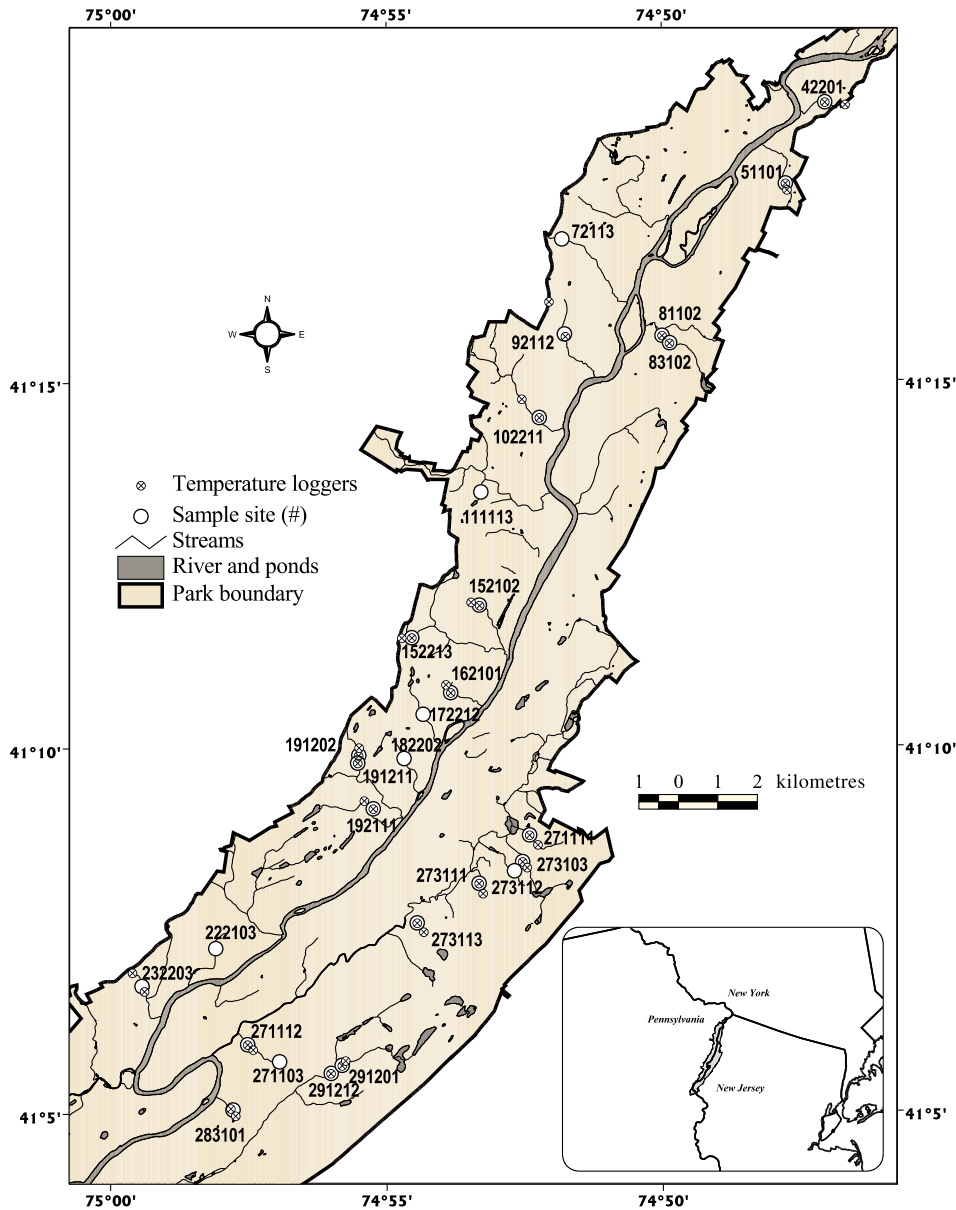
Delaware Water Gap National Recreation Area (DEWA) is located in northeastern Pennsylvania and western New Jersey (Fig. 1). The Park encompasses 27 742 ha of forested hills, ravines, and bottom lands straddling the Delaware River. A total of 21 885 ha of DEWA are forested: 18 575 ha are deciduous forest, 1295 ha are evergreen forest, and 2015 ha are mixed evergreen–deciduous forest (Myers and Irish 1981). The dominant hardwood species are red oak (*Quercus rubra*), followed by sugar maple (*Acer saccharum*), chestnut oak (*Quercus prinus*), red maple (*Acer rubrum*), and sweet birch (*Betula lenta*). Dominant evergreens are white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and red cedar (*Juniperus virginiana*).

Hemlock stands in DEWA are patchily distributed, occurring largely on relatively cool, moist sites. Though stands containing significant amounts of hemlock comprise only about 5% of the forested landscape in DEWA (1130 ha), where they occur, hemlock often dominates, comprising as much as 77% of the basal area in stands (Sullivan et al. 1998). Recent evidence suggests that before Euro-American settlement, hemlock represented a greater component of many northeastern U.S. forests than it does today and that present-day hemlock stands are often restricted to permanent woodlots with reduced disturbance histories (Foster et al. 1998; McLachlan et al. 2000). In DEWA, many hardwood stands, especially in ravine terrains, are younger on average than hemlock stands and contain a large number of cut, decayed hemlock stumps, suggesting that hemlock was likely once more abundant in DEWA as well (Sullivan et al. 1998).

Hemlock woolly adelgid (HWA) infestations were first detected in DEWA in 1989, and a subsequent survey conducted in 1995 indicated that over half of the Park's hemlock stands were infested (Evans 1995). Nevertheless, at the time of this study, HWA-induced mortality was limited to a few small stands, mostly in the southeastern portion of the Park. Since this study was conducted, impacts from HWA have increased dramatically (R. Evans, Delaware Water Gap National Recreation Area, Charles Pierce House, HC 38, Milford, PA 18337, personal communication).

The topographic setting of DEWA is varied, with terraced benches and ravines to the west, significant river bottom habitats surrounding the Delaware River, and steeply sloping ridge landforms to the east. The minimum elevation is approximately 84 m and maximum elevation is about 490 m. Nearly 60 km of the Delaware River flows through the Park. Additionally, the Park has 87 km of 1st-order streams, 32 km of 2nd-order streams, and 60 km of 3rd-order or higher streams, many of which originate outside the Park.

Fig. 1. Delaware Water Gap National Recreation Area (DEWA) depicting location of the Park (inset) and the study sites. Sites containing temperature loggers are also shown. Site numbers are a hierarchical coding system. First two digits refer to sub-basin number (sub-basins are numbered sequentially from north to south), the third digit refers to the terrain type (1 = bench; 2 = ravine; 3 = midslope), the fourth digit represents stream order (one or two); the fifth digit represents forest type (0 = hardwood; 1 = hemlock); and the sixth digit represents the replicate number (1, 2, or 3).



Landscape analysis and sampling design

Our approach was to focus the study on smaller, headwater catchments because larger streams drained areas containing both hemlock and mixed hardwood forest making forest-specific comparison intractable. In addition, most of these larger watersheds were impacted by humans (e.g., impoundments, agriculture, quarries), which could confound our assessment of the influence of hemlock. Even after limiting the study to headwater catchments, other possible confounding factors remained; we controlled for landscape variability (i.e., terrain and stream size) through the sampling design, and we excluded others (i.e., minimum catchment area, beaver activity) through site selection. Because the primary objective was to detect a forest-type effect, we chose to study

the endpoints represented by streams draining forest that were either dominated by hemlock or dominated by mixed hardwood. In this way, we maximized the opportunity to detect a forest-type effect if one existed.

We used geographic information systems (GIS) to characterize the landscape in DEWA and to provide the basis for the terrain-based, paired-site sampling design used in this study. Our goal was to sample across the range of landscape variability in the Park and control for the effects of terrain and stream size before comparing aquatic invertebrate community measures between forest types. Landscape analysis consisted of five steps: (i) classifying a digital vegetation map (Myers and Irish 1981) into two forest types (hemlock and mixed hardwood), (ii) characterizing the diversity of ter-

rain where hemlock occurs, (iii) assessing stream order and length by forest stand, (iv) defining landscape treatments based on forest type, terrain type, and stream order, and (v) pairing hemlock-dominated streams with similarly structured mixed hardwood dominated streams within each treatment (see Young et al. (2002) for a complete description).

We classified forest stands where hemlock represented the primary, secondary, or tertiary component of the stand as “hemlock” and classified stands with little or no hemlock as “hardwood”. Later ground surveys indicated that hemlock represented between 25 and 77% (median = 60%) of the total basal area of forests within watersheds above sample sites in selected hemlock stands and between 0 and 32% (median = 2%) within watersheds in selected hardwood stands (Sullivan et al. 1998).

We characterized terrain for each forest stand by deriving measures of elevation, slope, aspect, terrain shape, and solar radiance from a digital elevation model (Young et al. 2002). Subsequently, we used Euclidean distance based *k*-means clustering in SYSTAT (Wilkinson 1998) to classify hemlock stands into three types: bench, ravine, and midslope terrains (Young et al. 2002). Low mean slopes (i.e., topographically flat) distinguished bench sites from the other two terrains. Low terrain shape scores (i.e., watershed gorge-like or concave in cross section) distinguished ravines; and steep slopes, convex terrain shape, and relatively low solar radiance values distinguished midslope sites.

We quantified the length and order (Strahler 1964) of streams flowing through each forest stand using digital stream data (Young et al. 2002). A total of 56 hemlock and 333 hardwood stands contained 1st- and 2nd-order streams. There were hemlock stands in both bench and ravine terrains that contained 1st- and (or) 2nd-order streams. Stands in midslope terrains contained only 1st-order streams. We combined the three terrain types and two stream orders to form sampling strata (hereafter termed “stream types”). We designated the five stream types as follows: 1st-order bench, 2nd-order bench, 1st-order ravine, 2nd-order ravine, and 1st-order midslope.

Before selecting sample sites within each stream type, we imposed two additional constraints on site selection to maximize the probability of detecting a forest-type effect if one existed. First, we only considered hemlock or hardwood forest stands that were greater than a total area of 5 ha within a selected watershed. Second, we required that selected stands contain a minimum of 100 m of 1st-order or 200 m of 2nd-order stream length. We imposed these additional constraints because forest-type effects on aquatic assemblages would most likely be detectable in catchments where long reaches of stream drain a single dominant forest type. One additional hardwood stand was eliminated because there was substantial beaver activity within the watershed. As a result, 29 hemlock stands and 134 hardwood stands comprised our target population.

From the target population, we randomly selected three hemlock stands from each stream type, and then paired each one with a corresponding hardwood site that drained the same stream order and was most similar in terms of the five terrain variables (Young et al. 2002). Upon field inspection, one site-pair in the 2nd-order bench strata was dropped because of clear differences in discharge, leaving a total of 14

site-pairs. Young et al. (2002) found the terrain-based, paired-site study design effectively represented the diversity of environments where hemlock occurred in DEWA and significantly improved statistical inference and power over a simple random sampling design.

Macroinvertebrate sampling and processing

Invertebrate sampling was conducted during the first two weeks of April 1997. Originally, sampling was planned for mid-March. This period was selected to coincide with peak benthic diversity, before the onset of adult emergence for most aquatic insect species and when stream habitat is used most heavily by later instars (Plafkin et al. 1989). However, high stream flows prevented March sampling. Nevertheless, past studies of emergence patterns of aquatic insects inhabiting small, cold-water streams in the region suggest that peak emergence periods for most species occur after the early-April sampling period (Singh et al. 1984; Duffield and Nelson 1990; Masteller 1993). Thus, although emergence of some individuals may have occurred before sampling, it is likely that a significant fraction of individuals of most taxa were represented in the benthos. Furthermore, streams of each hemlock–hardwood site-pair were sampled either on the same day or only one day apart to control for temporal differences in community structure. Sample reaches were defined by a distance of 80 m for 1st-order streams and 160 m for 2nd-order streams. These distances represented approximately 40 mean stream widths and encompassed a minimum of three riffle–pool sequences.

Two approaches were used for invertebrate sampling. First, a combination of systematic and random sampling was used to obtain unbiased estimates of actual and relative abundances. A total of 20 equally spaced transects perpendicular to stream flow were established (i.e., 4 m apart for the 80-m 1st-order reaches and 8 m apart for the 160-m 2nd-order reaches). A single invertebrate sample was collected at a random location along each transect for a total of 20 samples per stream. Sampling consisted of 30-s kicks with a standard D-frame kick net (250 μ m mesh) over an area of 0.09 m² at each selected site. All 20 samples were combined into a single composite sample and preserved with 80% isopropyl alcohol in the field. Composite samples allowed us to sample more streams and a larger proportion of each stream for a given amount of effort. Because we were interested in comparing biological structure among stream types, as opposed to reaches within a single stream, composite sampling was justified.

Second, a qualitative, microhabitat-based approach was used to maximize the probability of collecting individuals of all species by sampling in all available microhabitats independent of their rarity. The classification approach that we used to define available microhabitats was based on water depth, velocity, and predominant substrate, variables known to be important determinants of aquatic invertebrate distributions (Minshall 1984; Newbury 1984). A rapid approach was used to distinguish microhabitats, relying on visually distinguishable differences in velocity (fast vs. slow water, turbulent vs. nonturbulent) and substrate (pea-sized vs. golf-ball-sized, etc), and easily measured differences in depth (>30 cm vs. <30 cm) (Table 1). Two investigators (one on each bank) searched the entire stream reach for the presence

of each of the 50 possible microhabitat types (Table 1). Individual microhabitats had to be a minimum of 1 m² to sample. Attempts were made to collect a minimum of two samples from each available microhabitat type. Qualitative samples were also collected with a D-frame kick net and were composited and preserved as described above for random samples.

In the laboratory, each composite sample (one random and one qualitative sample per site) was split into 16 subsamples by volume. The splitter consisted of a 2.5-gallon bucket centered over a large Plexiglas wedge. The bucket was mounted on a pivot so that it could be tipped evenly and sample contents could be dispersed over the wedge and collected in two large plastic receptacles. This procedure was repeated with each fraction until there were a total of 16 subsamples of approximately equal volume.

For each composite sample, invertebrates were picked, identified, and enumerated from four randomly selected subsamples (i.e., 25% of each composite sample). The 25% was chosen based on the results of an analysis that we conducted to determine the minimum number of subsamples required to accurately represent taxa richness and total abundance in the entire composite sample. Specifically, we determined taxa richness and total abundance for all 16 subsamples from two of the 56 composite samples. Subsequently, by computer, we randomly drew a bootstrap subsample (Manly 1991) from the total ($N = 16$) and calculated richness and abundance based on the bootstrap subsample. This process was repeated 1000 times for each subsample size (1, 2, 4, and 8). Results of this bootstrapping procedure indicated that taxa richness and total abundance estimated from four subsamples were within 10% of the true value of the entire sample 90% of the time.

Stream habitat sampling

In-stream habitat measurements were taken within the same stream reaches used to collect macroinvertebrates. Water chemistry measurements were taken at each site during spring high-flow conditions proximate to invertebrate sampling in well-mixed areas of high flow. Dissolved oxygen, pH, and specific conductance were measured using a Hydrolab Reporter multiprobe meter (Hydrolab Corp., Austin, Tex.), and turbidity was measured with a LaMotte turbidity meter (model 2008; LaMotte Co., Chestertown, Md.). Nutrients, including total nitrates, total nitrites, reactive phosphates, and ammonia, were measured using a direct-reading spectrophotometer (model DR/2000; HACH Co., Loveland, Colo.). Stream discharge was measured in the spring, during a prolonged period of high stream flows in an area of relatively laminar flow using a digital flowmeter (FloMate model 2000; Marsh-McBirney Inc., Frederick, Md.). Water temperature was measured hourly between 01 April 1997 and 31 March 1998 at 10 of the 28 sites (i.e., two replicate site-pairs for each of the five different stream types; Fig. 1) using Optic StowAway™ temperature loggers (Onset Computer Corp., Pocasset, Mass.). Loggers were placed near the bottom of the sample reaches where invertebrates were collected.

Stream channel measurements included (i) microhabitat diversity, (ii) large woody debris (LWD), and (iii) the extent to which each stream dried during the summer. Microhabitat

(classified as in Table 1) was determined at each of the 20 random locations where invertebrate samples were taken. Large woody debris was censused during summer base flow (08 July – 16 July). For each stream reach, all logs and sticks entirely or partially within the bankfull stream channel were classified according to size, based on length and diameter (Dolloff et al. 1993). Measurements were made on the entire log or stick even if only a portion occurred within the stream channel because we were interested in forest-type effects on LWD loading as well as available habitat for invertebrates. The proportion of a stream that dried during the summer was visually estimated to the nearest 10%. Each stream was subsequently classified into one of four categories based on the amount of the bankfull stream channel bottom that remained wetted: wet = completely wet; mostly wet = >50% of channel bottom wetted; mostly dry = <50% of channel bottom wetted; and dry = completely dry.

Statistical analyses

Two primary data matrices from the invertebrate samples were used for analyses. For analyses based on species abundances (e.g., density and relative abundance comparisons), we created a site × species abundance matrix using the random samples only. For analyses based on occurrence or richness of species, we created a presence–absence matrix using data from both the random and qualitative samples.

We compared four measures of invertebrate assemblage structure between streams draining hemlock and hardwood forests: (i) taxa richness, (ii) Simpson's evenness index (Brower and Zar 1984), (iv) total density, and (v) number of rare taxa (defined as taxa that occurred at fewer than four sites). Making use of the terrain-based, paired-site design (Young et al. 2002), we tested the null hypothesis that mean differences in each community structure metric between site-pairs were equal to zero. For each metric, we calculated the difference between individual hemlock–hardwood site-pairs by subtracting the value measured in the hardwood site from that in the corresponding hemlock site. We used analysis of variance (ANOVA) to determine if mean differences between forest types varied among stream types. This is analogous to testing the effect of the interaction between forest type and stream type on each response variable. In the absence of an interaction, we used a paired *t* test to test the main effect of forest type on assemblage structure. Differences approximated a normal distribution so no transformations were required before analysis. We used Systat (Wilkinson 1998) software to conduct ANOVA and paired *t* tests.

We also compared the taxonomic and trophic composition of aquatic invertebrate assemblages between forest types. For taxonomic composition, we conducted an odds ratio test (Agresti 1990) to determine the association between the presence of each taxon and forest type. The odds of taxon presence is the probability of presence divided by the probability of absence. There are two relevant odds: one specific to hemlock stands and the other specific to hardwood stands. The ratio of these odds is the odds ratio. The natural log of the odds ratio tends to make the statistic normally distributed and more easily interpretable. We computed odds ratios and *p* values using LogXact (Mehta and Patel 1996).

For trophic composition, we used multiresponse permutation procedure (MRPP) to analyze forest-type effect on the

Table 1. Microhabitat classification matrix used to stratify qualitative invertebrate sampling.

Substrate	Slow-water habitats				Fast-water habitats					
	Depth <30 cm		Depth >30 cm		Riffles-rapids		Runs		Waterfalls	
	HEM	HRD	HEM	HRD	HEM	HRD	HEM	HRD	HEM	HRD
Logs (>30 cm diameter)	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sticks (<30 cm diameter)	1.8	1.1	0.0	0.0	1.1	1.1	0.4	0.7	0.0	0.0
Leaf packs	1.8	3.2	0.0	0.0	0.0	1.4	0.4	1.8	0.0	0.0
Needle packs	< 0.1	0.0	0.0	0.0	0.4	0.0	0.4	0.0	0.0	0.0
Moss	0.4	0.7	0.0	0.0	5.0	3.2	1.4	1.4	0.0	1.8
Silt-detritus (not mineral) (<6.4 mm)	2.5	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sand (mineral, <pea sized) (<6.4 mm)	1.1	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gravel (mineral, pea – golf ball sized) (6.4–50 mm)	7.9	10.0	1.1	0.0	2.9	3.2	4.3	3.9	0.0	0.4
Cobble (mineral, golf ball – head sized) (50–200 mm)	12.5	8.9	0.4	0.0	20.0	18.9	8.9	14.3	0.0	0.0
Boulder-bedrock (mineral, >head sized) (>200 mm)	5.0	3.9	3.6	1.8	10.0	10.4	4.3	5.7	2.1	0.0

Note: Fast-water habitats were either turbulent (i.e., riffles, rapids, and waterfalls) or nonturbulent (runs). Slow-water habitats (i.e., pools) were either deep (i.e., >30 cm) or shallow. Depth was determined with a pole marked at 30 cm and velocity and turbulence were distinguished by visual inspection. Predominant substrate was classified into one of ten categories that were easily distinguished by eye. A total of 50 microhabitats were possible based on combinations of depth or water velocity and substrate. Percent of available habitat represented by each microhabitat type is shown for each forest type (HEM, hemlock; HRD, hardwood).

proportion of individuals in four trophic groups: shredder-detritivores, collector-detritivores, grazer-algivores, and predators (Merritt and Cummins 1996). MRPP is a nonparametric procedure designed to test for differences in multivariate responses among groups and has the advantage of not requiring multivariate normality and homogeneity of variance that are seldom met with ecological community data (Zimmerman et al. 1985). Initially, we tested whether forest-type effect was homogeneous among stream types. If the effect was homogeneous, we tested whether trophic composition varied between paired hemlock and hardwood stands. We computed MRPP test statistics and p values using BLOSSOM software (Cade and Richards 2000). We also compared paired differences in the proportion of individuals in each trophic group separately using ANOVA and paired t tests as we did for assemblage structure responses.

We evaluated the effect of forest type on stream habitat using the same methods as those used to compare aquatic invertebrate assemblage structure responses. We compared temperature patterns (means, maxima, and minima) of streams in hemlock and hardwood forest types graphically using the hourly temperature data collected with temperature loggers. Finally, we used logistic regression to determine the relationship between the probability of a stream drying and forest type. For all the tests of statistical significance described above, we used an alpha value of $P = 0.10$.

Results

Interaction between stream and forest types

The effect of forest type did not depend on stream type for most biological and stream-habitat responses. Forest-type effect on density, number of rare species, and trophic composition were homogeneous among stream types (density,

$F_{[4,9]} = 0.62$, $p = 0.66$; rare species, $F_{[4,9]} = 2.24$, $p = 0.15$; trophic composition, $\delta = 2.15$, $p = 0.15$). Likewise, forest-type effect did not vary among stream types for any of the eight water chemistry variables ($p > 0.27$ for all variables) or in the frequency of LWD in any of the seven size classes or for the total ($p > 0.36$ for all size classes).

In contrast, forest-type effect on taxa richness and Simpson's evenness index did depend on stream type (taxa richness, $F_{[4,9]} = 3.27$, $p = 0.07$; Simpson's evenness, $F_{[4,9]} = 3.32$, $p = 0.06$). Differences between hemlock-hardwood site-pairs in microhabitat diversity also varied among stream types ($F_{[4,9]} = 4.73$, $p = 0.02$), and graphical examination of temperature data suggested that differences in thermal patterns between hemlock and hardwood sites were not independent of stream type. Plots of mean differences by stream type suggested that for response variables where forest-type effect depended on stream type, 1st-order midslope sites showed a different pattern than the other four stream types. In some cases (Simpson's evenness index and temperature patterns), midslope sites showed a pattern opposite that shown by the other stream types, and in others, midslope sites showed no difference or a much smaller mean forest-type difference than the other stream types (taxa richness and microhabitat diversity). We retested the effect of stream type on forest-type differences with midslope sites excluded and found that differences between hemlock-hardwood site-pairs no longer depended on stream type when midslope sites were excluded ($p > 0.20$ for all variables).

In addition, midslope sites represented only a small component of the Park landscape (only five of the 142 hemlock stands in the Park that contained 1st- or 2nd-order streams were classified as midslope). Because all biological and stream-habitat responses were homogeneous among all but midslope stream types and because midslope stream types were rare in the Park, we removed midslope sites from the

analysis and pooled the data from the remaining four stream types. Thus, for the rest of the paper, we discuss results from other than midslope sites.

Aquatic invertebrate community structure

A total of 151 taxa were positively identified from benthic samples; 43 taxa were identified to species, 94 to genus, 13 to family, and 1 to order. The number of taxa collected at any one site ranged between 21 and 66. A total of 64 taxa were considered rare (i.e., occurred at fewer than four sites), and the number of rare taxa ranged between 0 and 10. A total of 53 868 individuals were collected, and density ranged between 116 and 4698 individuals·m⁻².

Analysis of data pooled across stream types excluding 1st-order midslope sites indicated that all four invertebrate community structure measures were highly variable, even within a forest type (Fig. 2a). Despite the large variances observed within forest types, mean differences between hemlock–hardwood site-pairs were significantly different from zero for all four response variables (Fig. 2b). Streams draining hemlock supported on average about 1.5 times more total taxa (mean difference = 14 taxa) and had nearly 9% higher Simpson evenness indices than streams draining hardwood forests. In contrast, streams draining hardwood forests were over 2.7 times more dense (mean difference = 838 individuals·m⁻²) and supported more rare taxa (mean difference = 2 taxa) than streams draining hemlock.

Results of odds ratio tests for each taxon indicated that forest-specific differences in taxa richness were associated with specific taxa and were not simply a random subset of the community. Eleven taxa (7.3% of total) showed strong associations with hemlock (odds ratio test, $p < 0.10$), whereas no taxa were strongly associated with hardwood forests (Table 2). An additional 17 taxa showed weaker associations with hemlock (odds ratio test, $p < 0.30$), whereas only five taxa showed weak associations with hardwood forests (Table 2). Of the 28 taxa that showed either strong or weak associations with hemlock, three were found to occur exclusively in hemlock-dominated watersheds, whereas no taxa were found to occur in streams only draining hardwood forests.

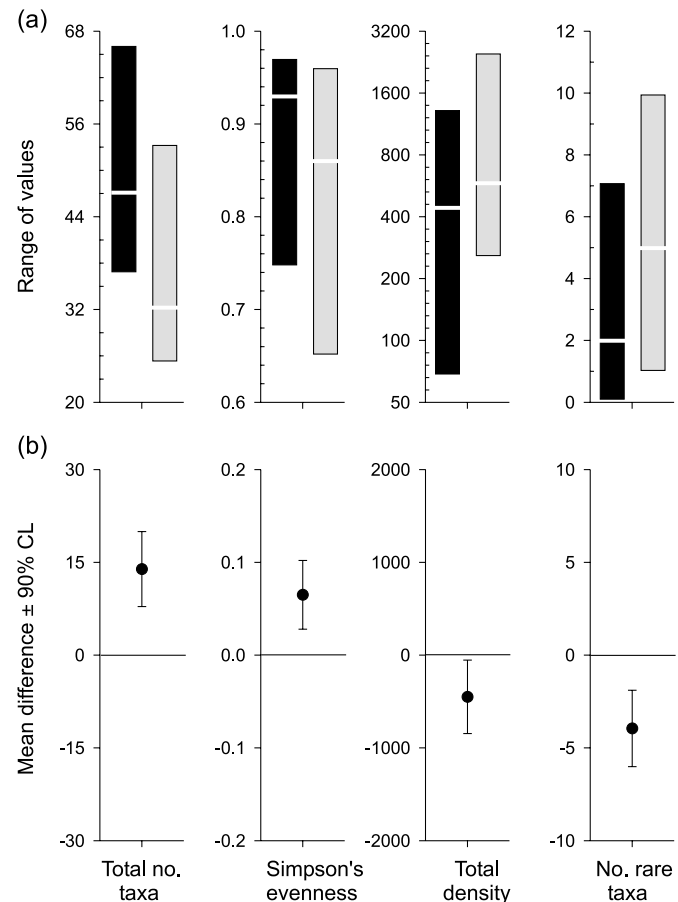
Trophic composition (i.e., the proportion of individuals in each of the four trophic groups) also differed between streams draining hemlock and hardwood forests ($\delta = 2.18$, $p = 0.009$). Predators comprised a significantly larger fraction and grazer–algivores comprised a significantly smaller fraction of the invertebrate assemblage in hemlock-drained streams (Fig. 3). The proportion of individuals as shredders and collectors did not differ between forest types.

Stream habitat

Water chemistry was highly variable among DEWA streams, with several variables exceeding an order of magnitude in range (Table 3). However, mean differences between hemlock–hardwood site-pairs were not significantly different from zero for any of the eight water chemistry variables measured (Table 3). Similarly, forest type did not affect spring discharge, microhabitat diversity, or the frequency of large wood debris (Table 3).

Median daily stream temperatures at hemlock sites tended to be cooler in the summer, warmer in the winter, and less

Fig. 2. Comparison of four community structure metrics between streams draining hemlock and mixed hardwood forests. (a) Comparison of the range of values (limits of boxes) and medians (white lines) for each metric between streams draining hemlock (solid bars) and hardwood (shaded bars) forests. (b) Depiction of the average difference ($\pm 90\%$ confidence limits, CL) between hemlock–hardwood site-pairs. Positive values indicate higher means for hemlock. Comparisons exclude 1st-order midslope sites, which exhibited distinctly different patterns than the other stream types (see text).



variable throughout the year (Fig. 4). In addition, summer daily maxima were lower and winter daily minima were higher in hemlock-drained streams. For example, summer daily maxima in streams draining hardwood forests exceeded 20°C 18% of the time compared with less than 3% in streams draining hemlock, and winter minimum daily temperatures dropped below freezing 8% of the time in hardwood sites compared with only 0.2% in hemlock sites (Fig. 5).

We used flow data from the USGS (U.S. Geological Survey) gaging station on the Bushkill River to characterize long-term rainfall patterns in the Park. We found stream flows to be normal (i.e., close to the long-term average) during the spring of 1997, when invertebrate sampling was conducted. However, the summer of 1997 was very dry with stream flows during the months of July and August falling well below what would be considered normal for that time of year. Specifically, over the 90-year period between 1908

Table 2. Identity of taxa with forest type preferences.

Strong hemlock associates	Weak hemlock associates	Weak hardwood associates
<i>Baetis amplus</i>	<i>Ephemerella</i> sp.	<i>Allocapnia</i> sp.
Leptophlebiidae	<i>Eurylophella</i> sp.	<i>Prostoia similis</i>
<i>Lanthus parvulus</i>	<i>Leuctra</i> sp.	<i>Chaetocladius</i> sp.
Perlidae	<i>Isoperla</i> sp.	<i>Diplocladius</i> sp.
<i>Hydropsyche ventura</i> *	<i>Diplectrona modesta</i>	<i>Tipula</i> sp.
<i>Bezzia</i> sp.	<i>Lepidostoma</i> sp.	
<i>Brillia</i> sp.	Limnephilidae	
<i>Psilometriche</i> sp.	<i>Polycentropus</i> sp.*	
<i>Rheocricotopus</i> sp.	<i>Rhyacophila minora</i>	
<i>Hexatoma</i> sp.	<i>Promoresia</i> sp.	
<i>Pseudolimnophila</i> sp.	<i>Ectopria nervosa</i>	
	<i>Natarsia</i> sp.*	
	<i>Polypedilum</i> sp.	
	<i>Stempellinella</i> sp.	
	<i>Symbiocladius</i> sp.	
	<i>Molophilus</i> sp.	
	<i>Psidium</i> sp.	

Note: Strong preference defined as p values of less than 0.1 in odds ratio test (see Methods). Weak preferences defined as p values less than 0.30. The asterisks (*) indicate taxa found only in streams draining hemlock. There were no strong hardwood associates.

and 1997, only 5.5% of the average flows in July and 6.6% of the average flows in August were as low or lower than those observed in 1997. The result of the dry summer in 1997 was that a substantial portion of our study streams dried completely. We observed forest-specific differences in the extent to which streams dried. In the summer of 1997, 9 of 14 (64%) streams draining hardwood forests became dry or mostly dry, whereas 2 of 14 (14%) streams draining hemlock dried partially. None of the streams draining hemlock dried completely compared with 4 of 14 (29%) streams draining hardwood. Weather patterns during the summer of 1999 were even more severe, with the month of July being one of the driest on record. At our request, DEWA personnel revisited our study sites in July of 1999 and determined which sites remained wet (i.e., contained some water and positive flow). They found 6 of 14 (43%) streams draining hardwood dried completely compared with only 1 of 14 (7%) streams draining hemlock (R. Evans, Delaware Water Gap National Recreation Area, Charles Pierce House, HC 38, Milford, PA 18337, personal communication).

The probability of a stream becoming dry or mostly dry during the summer of 1997 was related to two variables measured: forest type and spring high flows. The likelihood that a stream would dry was higher when the previous spring flows were low (Fig. 6). However, streams draining hemlock were much less likely to dry over a wide range of high-flow discharges. The critical spring flow (i.e., spring discharge where the likelihood of becoming dry exceeds the likelihood of remaining wet) was an order of magnitude lower for streams draining hemlock forests (Fig. 6).

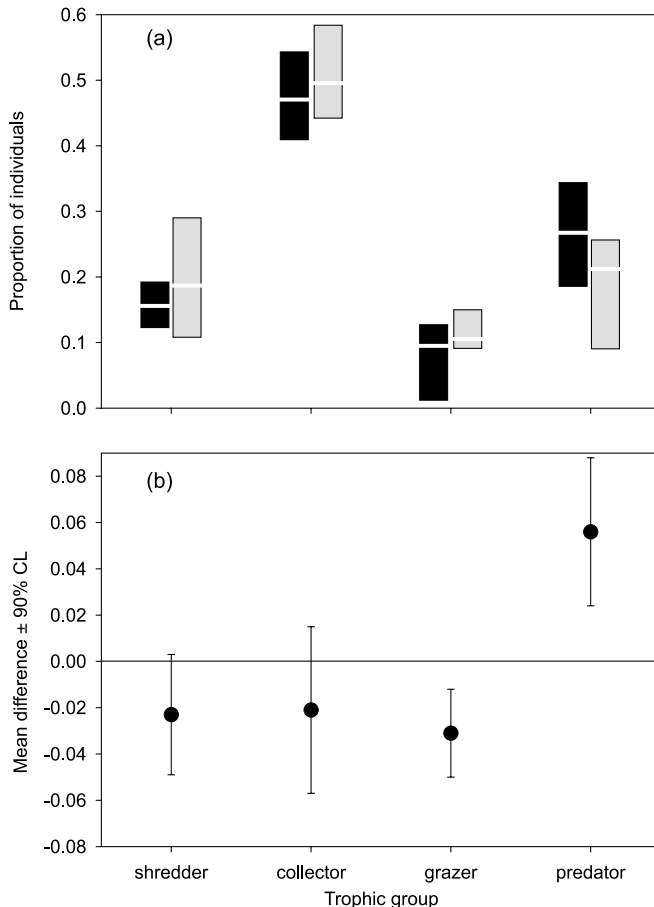
Discussion

After accounting for differences in terrain and stream order, we found that aquatic invertebrate community structure was significantly different between streams draining hemlock and those draining mixed hardwood forests. Streams

draining hemlock forests supported more total taxa than those draining hardwood forests, and over 7% of the taxa showed strong associations with hemlock, including three taxa found exclusively in hemlock streams. These patterns suggest that both within-site and park-wide diversity of aquatic invertebrates were enhanced by hemlock or by factors correlated with hemlock. In addition, invertebrate taxa were distributed more evenly (i.e., higher Simpson's evenness values) in hemlock-drained streams, indicating that higher richness values were not associated with the chance occurrence of taxa represented by relatively few individuals. In contrast, the number of rare taxa and total densities were lower in streams draining hemlock, suggesting that diversity differences were not related to stochastic factors associated with sampling (e.g., richness related to number of individuals collected or chance occurrence of rare species) and that streams draining hardwood forests may have been more productive.

Few studies have investigated the influence of hemlock forests on aquatic communities. In a study comparing leaf decomposition rates, Maloney and Lamberti (1995) found that hemlock needles decayed slower and supported fewer macroinvertebrates than the leaves of four other riparian plant species in a northern Michigan stream and suggested that hemlock may contain secondary compounds that inhibit decomposition. Comparative and experimental studies with other conifer species (mainly *Pinus*) suggest that conifer needles are relatively poor food sources and are generally avoided by leaf-shredding insects (Webster and Benfield 1986). However, Bowen et al. (1995) found that hemlock logs and branches supported relatively high densities of chironomids and other invertebrates in the littoral zone of two lakes in eastern Canada; but based on species composition (i.e., low proportion of shredders and high proportion of filter feeders and collectors), they hypothesized that colonizing invertebrates were using wood debris mainly as a substrate rather than as a food source. Boucherle et al. (1985) studied

Fig. 3. Comparison of the proportion of individuals in each of four trophic groups. (a) Comparison of the range of values (limits of boxes) and medians (white lines) for each metric between streams draining hemlock (solid bars) and hardwood (shaded bars) forests. (b) Depiction of the average difference ($\pm 90\%$ confidence limits, CL) between hemlock–hardwood site-pairs. Positive values indicate higher means for hemlock. Comparisons exclude 1st-order midslope sites, which exhibited distinctly different patterns than the other stream types (see text).



the limnologic consequences of the widespread hemlock decline that occurred during the mid-Holocene period (about 4800 years ago) in three southern Ontario lakes and found that lake trophic status and the species composition of plankton assemblages were altered by historic declines in hemlock forests. Our data suggest that similarly large changes may occur to aquatic invertebrate assemblages in headwater stream ecosystems should hemlock decline continue.

We observed differences in stream habitat that could explain differences in benthic macroinvertebrate diversity observed between forest types. Diel and seasonal thermal regimes were more moderate in hemlock-drained streams, and streams draining hardwood forests were more prone to drought disturbance than those draining hemlock. Higher frequency of subzero temperatures observed in hardwood-drained streams could promote the formation of anchor ice, which has been found to be a major factor regulating benthic assemblages by reducing taxa richness and limiting reproductive habitat (Miller and Stout 1989; Sahade et al. 1998). Moreover, more stable thermal regimes may help minimize

exposure of benthic communities to temperatures outside the optimum range for many component species. Although benthic macroinvertebrate diversity has been found to be positively related to thermal heterogeneity at the basin-wide or river-system scale (reviewed in Ward and Stanford 1982), there is evidence that benthic assemblages in headwater streams are more diverse in cooler, more thermally static streams. For example, Kamler (1965) characterized headwater mountain streams in Poland based on thermal patterns and found that streams with more variable thermal regimes supported fewer total taxa than streams with more static thermal regimes and attributed this pattern to the fact that the diversity of two important orders, Ephemeroptera and especially Plecoptera, are comprised of predominantly cold stenothermal species.

Greater stability of summer base flows in hemlock-drained streams may have contributed to forest-type differences in benthic diversity. Fewer streams draining hemlock forests dried up during two separate drought years, and the probability of drying was lower for streams draining hemlock. Moreover, these associations were independent of stream size, which was accounted for in the stratification and pairing procedures of the study design, or high-flow (spring) discharges, which were accounted for post hoc with regression analysis.

There is little doubt that stable base flows would afford, at least, short-term benefits to stream invertebrate communities. Because most aquatic insect species require at least 1 year to complete their life cycle (Wallace 1996), stream drying would likely kill or displace a large fraction of the benthic community leading to lower densities and diversity. Moreover, even if streams do not dry completely, partial drying would likely reduce available habitat to a series of small pools with little or no flow between them. Remaining refuges would likely be more vulnerable to density-dependent sources of mortality such as competition and predation (Power et al. 1988) and at greater risk to environmental extremes such as high water temperature and low dissolved oxygen levels (Lake and Boulton 1990).

In the longer term, disturbances such as droughts and floods could have either beneficial or detrimental effects on diversity depending on their timing, frequency, and severity. The role of disturbance in structuring natural communities has received considerable attention (e.g., Connell 1978; Huston 1979; Sousa 1984), and although there is general agreement that disturbance plays a significant, possibly overriding, role in structuring stream communities, no consensus has been reached regarding the specific mechanism (Resh et al. 1988; Death and Winterbourn 1995). Nevertheless, it is clear that disturbances may cause lasting reductions in the diversity of stream communities if they are severe enough to significantly depress exposed populations and widespread and frequent enough to limit recolonization from unaffected areas (Yount and Niemi 1990).

Hemlock and mixed hardwood forests also differ in their effect on autochthonous and allochthonous sources of energy, and these differences may explain observed differences in total invertebrate density and trophic composition observed between forest types. Streams draining hardwood forests receive more sunlight on an annual basis than those draining hemlock forests because of reduced shading associ-

Table 3. Comparison of water chemistry and physical habitat variables between hemlock (Hem) and mixed hardwood (Hrd) site-pairs in DEWA streams.

Variable	Range of values		Mean difference, Hem – Hrd	<i>p</i> value
	Hemlock	Hardwood		
Water chemistry				
Dissolved oxygen (mg·L ⁻¹)	11.4–13.5	10.3–13.8	0.5	0.29.
Specific conductance (ms·cm ⁻¹)	15–151	20–193	–33	0.18
pH (–log H ⁺ ions) ^a	5.70–7.52	5.74–7.98	8.38E-8	0.60
Turbidity (Nephelometric units)	0.10–6.74	0.10–12.50	–1.28	0.33
Ammonia (mg·L ⁻¹)	0.01–0.31	0.01–0.24	–0.01	0.88
Total nitrates (mg·L ⁻¹)	0.0–1.2	0.0–1.4	–0.1	0.79
Total nitrites (mg·L ⁻¹)	0.000–0.002	0.000–0.004	–0.001	0.12
Orthophosphates (mg·L ⁻¹)	0.00–0.28	0.00–0.28	–0.00	0.36
Physical habitat				
Spring discharge (m ³ ·s ⁻¹)	8.4–985.6	1.4–1070.5	0.3	0.67
Microhabitat diversity ^b	6–14	6–12	0	0.31
LWD (No.·100 m ⁻¹) ^c				+>
LWD: total	35–160	37–154	9	0.94
LWD: size class 1	15–71	8–86	9	0.53
LWD: size class 2	5–69	4–36	5	0.59
LWD: size class 3	0–3	0–6	0	0.36
LWD: size class 4	0–6	0–8	–2	0.18
LWD: size class 5	1–12	1–20	–1	0.79
LWD: size class 6	0–7	0–2	0	0.39
LWD: root wads	2–38	4–55	–2	0.44

Note: The range of values in each forest type, mean difference between site-pairs, and *p* values of *t* tests that test the null hypothesis that the average difference between hemlock–hardwood site-pairs is equal to zero are reported. Values observed in hardwood sites were subtracted from values in hemlock sites, so positive mean differences indicate that hemlock was higher. Midslope site-pairs were excluded from all analyses, so degrees of freedom were 10 for all tests.

^aRange of pH values are reported but the *t* test was conducted using [H⁺] instead of pH and the mean difference between site-pairs reported in the table is [H⁺].

^bMicrohabitat diversity refers to the number of microhabitat types as described in Table 1.

^cLWD refers to large woody debris (i.e., sticks and logs) found within the stream channel and differences in the frequency of LWD between hemlock–hardwood site-pairs were tested for the total (all LWD sizes classes summed) and for six separate size classes and root wads. Size classes were defined by combinations of diameter (cm) and length (m) as follows: size class 1, D = 5–10 cm, L = 1–5 m; size class 2, D = 10–50 cm, L = 1–5 m; size class 3, D = >50 cm, L = 1–5 m; size class 4, D = 5–10 cm, L = >5 m; size class 5, D = 10–50 cm, L = >5 m; size class 6, D = >50 cm, L = >5 m. Root wads refer to tree roots on stream banks capable of providing cover for fish.

ated with seasonal leaf-off periods, and even during leaf-on periods, hemlock forests filter out more sunlight than mixed hardwood forests (Hadley 2000). Because light appears to be the primary factor limiting primary production in these forested headwater stream environments (Hill and Knight 1988; Wellnitz et al. 1996), increases in incident light would stimulate more algal production, potentially increasing the total energy inputs and broadening the food base for stream invertebrates (Minshall 1978; Lamberti and Steinman 1997). Our observation that grazing algivores represented a larger fraction of the benthic community in hardwood-drained streams suggests an assemblage response to higher primary production. Smock and MacGregor (1988) showed that similar changes in trophic composition may have occurred following changes in forest composition resulting from the chestnut blight of the early 1900s.

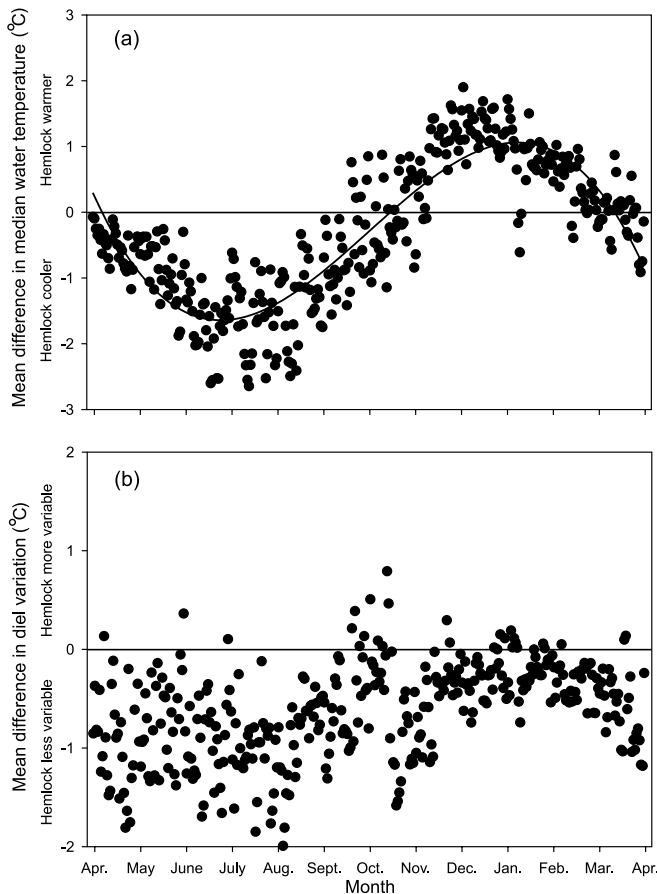
Although there is some evidence that hemlock and other conifers contribute more allochthonous inputs annually than mixed hardwood forests (Anderson and Sedell 1979; Molles 1982), much of that energy is not available as food for aquatic macroinvertebrates (Webster and Benfield 1986), and so hemlock forests may provide less usable allochthonous energy than mixed hardwood forests. Thus, in addition to more autochthonous-derived energy, greater contributions of

high-quality leaf litter may also contribute to the higher total abundances of benthic invertebrates that we observed in hardwood-drained streams.

Taken together, the results of the present study indicate that headwater streams drained by hemlock and mixed hardwood forests support substantially different benthic communities. Further, our results suggest that forest-type differences in light and temperature regimes, stability of summer base flows, and quality of allochthonous inputs are proximate causes of observed differences in benthic assemblage structure and composition. Based on these associations, we predict that pest-induced declines in hemlock will have long-term consequences for aquatic invertebrate assemblages including a reduction in both alpha (i.e., within-stream) and gamma (i.e., park-wide) aquatic invertebrate diversity, and possibly local increases in primary and secondary production.

It is also possible that more moderate thermal regimes and stable base flows were responsible for, rather than a consequence of, the occurrence of hemlock. Although we attempted to account for the effects of landscape determinants in the sampling design, there may have been variables that were not correlated with those that we used to stratify our sampling that were important determinants of both hemlock occurrence and aquatic invertebrate assemblage structure. In

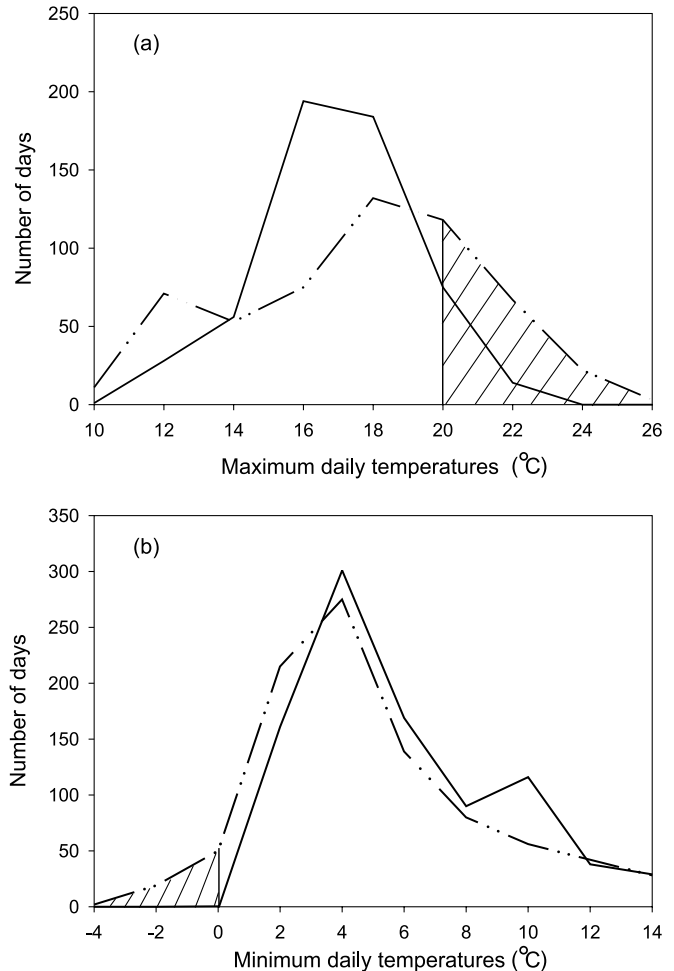
Fig. 4. Mean differences in (a) median daily temperature and (b) mean diel temperature range between hemlock–hardwood site-pairs. Data were pooled across stream types except for midslope site-pairs, which were not included because they showed a substantially different pattern (see text). Data from the hardwood site of each site-pair was subtracted from its corresponding hemlock site, so values greater than zero indicate that hemlock was (a) warmer and (b) more variable. Each data point represents the mean difference between six pairs of temperature loggers for a day.



particular, forest-type differences in the proportion of stream flow made up by groundwater could also explain the data. Streams with greater groundwater contributions often have attenuated thermal regimes and are less likely to dry up during droughts (Gordon et al. 1992). In turn, such systems may provide the cool, moist conditions conducive to hemlock growth as well as support more invertebrate species. In this case, hemlock woolly adelgid induced hemlock decline may have little effect on stream communities in the long term.

However, there is evidence to support the argument that hemlock is at least partially responsible for observed patterns in stream habitat and benthic community structure. For example, it has been shown that the deep shade provided by the dense canopy of hemlock stands produces a cooler, damper microclimate in the forest understory relative to other conifer and deciduous forests (Rogers 1978; Hadley 2000). Such conditions could potentially buffer summer stream temperature increases and reduce evaporation rates. In addition,

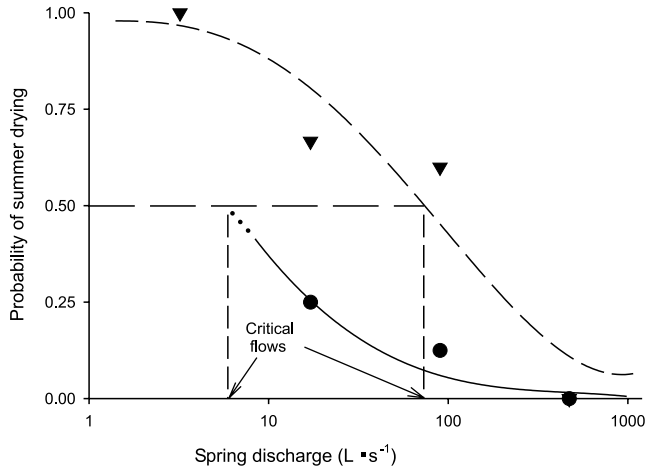
Fig. 5. Comparison of the distributions of (a) summer (July–September) maximum temperatures and (b) winter (October–February) minimum temperatures between streams draining hemlock and mixed hardwood forests. Solid lines depict hemlock data and broken lines depict hardwood data. Vertical lines represent arbitrary thresholds at 20°C and 0°C for comparisons. Data from temperature loggers placed at midslope sites were excluded because they showed different patterns than other stream types (see text).



Blair et al. (1994) showed that soils in hemlock forests have a greater moisture-holding capacity than those in mixed hardwood forests, which could result in a more gradual and stable runoff of surface water and more consistent recharge of groundwater aquifers during summer droughts. Finally, many of the mixed hardwood stands in this study were probably once dominated by hemlock that was cleared earlier in the century and replaced by mixed hardwood (Sullivan et al. 1998). This was especially evident in the hardwood ravines where old hemlock stumps and logs were ubiquitous. One would expect that these hardwood stands that were formerly hemlock would have similar groundwater inputs. Therefore, if groundwater sources play a role, then hemlock forests probably influence groundwater contributions in some way.

Thus, there appears to be a strong likelihood that replacement of hemlock stands in DEWA with mature mixed hard-

Fig. 6. Probability of streams becoming dry or mostly dry as a function of discharge of the previous spring and forest type. Actual data represented by symbols were computed by putting spring discharges into four bins or ranges (centered around 3, 17, 90, and 472 L·s⁻¹) and plotting the proportion of sites of each forest type that became dry or mostly dry in each discharge range. We used logistic regression to derive predicted probabilities from the data (represented by lines). Solid line depicts hemlock and broken line depicts hardwood sites.



wood stands will have long-term impacts on aquatic communities similar in magnitude to those that have been noted for terrestrial assemblages. Moreover, if hemlock is indeed the ultimate cause of observed patterns in stream habitat and benthic community structure, then predicted changes in the habitat and biological structure of these headwater ecosystems may have a significant influence on other aquatic assemblages throughout the drainage basin. For example, warmer summer temperatures may decrease the abundance and limit the distribution of brook trout (*Salvelinus fontinalis*), an important game species in the Park (Evans 1995). Brook trout spawning is restricted to water of $\leq 15^{\circ}\text{C}$, and adults rarely occur in streams where summer temperatures exceed 20°C (Jenkins and Burkhead 1993). Also, reductions in thermal and hydrologic stability in tributaries could affect the survival and productivity of Delaware River mainstem fishes, such as trout and shad, that may be limited by the relative severity of summer, base-flow conditions. Stable discharges of cooler water from hemlock-dominated sub-basins may provide refugia during these summer extremes.

Acknowledgments

We thank R. Evans, E. Johnson, A. Ambler, K. High, and J. Schreiner of the Delaware Water Gap National Recreation Area for providing digital maps and logistical support for fieldwork. Comments provided by E. Pendleton, E. Benfield, R. Evans, D. Morton, and Z. Johnson were valuable in improving the manuscript. Funding for the research was obtained through the National Park Service's Natural Resources Preservation Program (NRPP).

References

- Agresti, A. 1990. Categorical data analysis. John Wiley and Sons, New York.
- Anderson, N.H., and Sedell, J.R. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annu. Rev. Entomol.* **24**: 351–377.
- Blair, J.M., Parmelee, R.W., and Wyman, R.L. 1994. A comparison of the forest floor invertebrate communities of four forest types in the northeastern U.S. *Pedobiologia*, **38**: 146–160.
- Bosakowski, T., Smith, D.G., and Speiser, R. 1992. Nest sites and habitat selected by Cooper's hawks, *Accipiter cooperii*, in northern New Jersey and southeastern New York. *Can. Field-Nat.* **106**: 474–479.
- Boucherle, M.M., Smol, J.T., Oliver, T.C., Brown, S.R., and McNeely, R. 1985. Limnologic consequences of the decline in hemlock 4800 years ago in three southern Ontario lakes. *Paleolimnology*, **143**: 217–225.
- Bowen, K.L., Kaushik, N.K., Gordon, A.M., Mallory, E., Ridgeway, M., Bachmann, R.W., Jones, J.R., Peters, R.H., and Soballe, D.M. 1995. Invertebrate colonization of coarse woody debris in the littoral zone of two oligotrophic lakes. *Lake Reservoir Manag.* **11**: 119–120.
- Brower, J.E., and Zar, J.H. 1984. Field and laboratory methods for general ecology. 2nd ed. William C. Brown Publishers, Dubuque, Iowa.
- Cade, B.S., and Richards, J.D. 2000. User manual for BLOSSOM statistical software. Midcontinent Ecological Research Center, United States Geological Survey, 4512 McMurray Avenue, Fort Collins, CO 80525-3400, U.S.A.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science (Washington, D.C.)*, **199**: 1302–1310.
- Cuffney, T.F., Wallace, J.B., and Lughart, G.J. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshwater Biol.* **23**: 281–299.
- Death, R.G., and Winterbourn, M.J. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology*, **76**: 1446–1460.
- Dolloff, C.A., Hankin, D.G., and Reeves, G.H. 1993. Basinwide estimation of habitat and fish populations in streams. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experimental Station, Asheville, NC 28804. General Technical Report SE-83.
- Duffield, R.M., and Nelson, C.H. 1990. Seasonal emergence patterns and diversity of Plecoptera on Big Hunting Creek, Maryland, with a checklist of the stoneflies of Maryland. *Proc. Entomol. Soc. Wash.* **92**: 120–126.
- Evans, R.A. 1995. Hemlock ravines at Delaware Water Gap National Recreation Area: highly valued, distinctive and threatened ecosystems. In Delaware Water Gap National Recreation Area 30th Anniversary symposium. Available from Richard Evans, National Park Service, Delaware Water Gap National Recreation Area, 294 Old Milford Rd., Milford, PA 18337.
- Foster, D.R., Motzkin, G., and Slater, B. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems*, **1**: 96–119.
- Fuller, J.L. 1998. Ecological impact of the mid-Holocene hemlock decline in southern Ontario, Canada. *Ecology*, **79**: 2237–2351.
- Gordon, N.D., McMahon, T.A., and Finlayson, B.L. 1992. Stream hydrology: an introduction for ecologists. John Wiley and Sons Ltd, West Sussex, England.
- Gregory, K.J. 1992. Vegetation and river channel process interactions. In River conservation and management. Edited by P.J.

- Boon, P. Calow, and G.E. Petts. John Wiley and Sons Limited, West Sussex, England. pp. 255–269.
- Griesemer, S.J., Fuller, T.K., and Degraaf, R.M. 1998. Habitat use by porcupines (*Erethizon dorsatum*) in central Massachusetts: effects of topography and forest composition. *Am. Midl. Nat.* **140**: 271–279.
- Hadley, J.L. 2000. Understory microclimate and photosynthetic response of saplings in an old-growth eastern hemlock (*Tsuga canadensis* L.) forest. *Ecoscience*, **7**: 66–72.
- Hill, W.R., and Knight, A.W. 1988. Nutrient and light limitation of algae in two northern California streams. *J. Phycol.* **24**: 125–132.
- Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.* **113**: 81–101.
- Jackson, J.K., and Fisher, S.G. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. *Ecology*, **67**: 629–638.
- Jenkins, R.E., and Burkhead, N.M. 1993. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.
- Kamler, E. 1965. Thermal conditions in mountain waters and their influence on the distribution of Plecoptera and Ephemeroptera larvae. *Ekol. Pol. Ser. A*, **13**: 377–414.
- Lake, P.S., and Boulton, A.J. 1990. Ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biol.* **24**: 123–141.
- Lamberti, G.A., and Steinman, A.D. 1997. A comparison of primary production in stream ecosystems. *In Stream organic matter budgets. Edited by J.R. Webster and J.L. Meyer. J. North Am. Benthol. Soc.* **16**: 3–16.
- Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W., and Pierce, R.S. 1970. The effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol. Monogr.* **40**: 23–47.
- Maloney, D.C., and Lamberti, G.A. 1995. Rapid decomposition of summer-input leaves in a northern Michigan stream. *Am. Midl. Nat.* **133**: 184–195.
- Manly, F.J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall Publishers, New York.
- Masteller, E.C. 1993. Comparison of tropical and temperate emergence phenology of aquatic insects from Puerto Rico and Pennsylvania. *J. Kans. Entomol. Soc.* **66**: 192–199.
- McClure, M.S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environ. Entomol.* **20**: 258–264.
- McLachlan, J.S., Foster, D.R., and Menalled, F. 2000. Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology*, **81**: 717–733.
- Mehta, C., and Patel, N. 1996. LogXact for Windows. User manual. Cytel Software Corporation, Cambridge, Mass., U.S.A.
- Merritt, R.W., and Cummins, K.W. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- Miller, M.C., and Stout, J.R. 1989. Variability of macroinvertebrate community composition in an Arctic and Subarctic stream. *Hydrobiologia*, **172**: 111–127.
- Minshall, G.W. 1978. Autotrophy in stream ecosystems. *BioScience*, **28**: 767–771.
- Minshall, G.W. 1984. Aquatic insect–substratum relationships. *In The ecology of aquatic insects. Edited by V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York.* pp. 358–400.
- Mitchell, J.M. 1999. Habitat relationships of five northern bird species breeding in hemlock ravines in Ohio, U.S.A. *Nat. Areas J.* **19**: 3–11.
- Molles, M.C. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. *Ecology*, **63**: 1–6.
- Myers, W.L., and Irish, R.R. 1981. Vegetation survey of Delaware Water Gap National Recreation Area. Final Report, U.S. Department of the Interior, National Park Service, Mid-Atlantic Region. Available from Richard Evans, National Park Service, Delaware Water Gap National Recreation Area, 294 Old Milford Rd., Milford, PA 18337.
- Naiman, R.J., Décamps, H., Pastor, J., and Johnston, C.A. 1988. The potential importance of boundaries to fluvial ecosystems. *J. North. Am. Benthol. Soc.* **7**: 289–306.
- Newbury, R.W. 1984. Hydrologic determinants of aquatic insect habitats. *In The ecology of aquatic insects. Edited by V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York.* pp. 323–357.
- Orwig, D.A., and Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, U.S.A. *J. Torrey Bot. Soc.* **125**: 60–73.
- Orwig, D.A., and Foster, D.R. 1999. Stand, landscape, and ecosystem analyses of hemlock woolly adelgid outbreaks in southern New England: an overview. *In Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. Edited by D.A. McManus, D.S. Shields, and D.R. Souto. U.S. Department of Agriculture, Forest Service, Newton Square, Pa.* pp. 123–125.
- Plafkin, J.L., Barbour, M.T., Porter, K.D., Gross, S.K., and Hughes, R.M. 1989. Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. United States Environmental Protection Agency, Washington, DC 20460. EPA/444/4-89-001.
- Power, M.E., Stout, R.J., Cushing, C.E., Harper, P.P., Hauer, F.R., Matthews, W.J., Moyle, P.B., Stutzner, B., and Wais De Badgen, I.R. 1988. Biotic and abiotic controls in river and stream communities. *J. North Am. Benthol. Soc.* **7**: 456–479.
- Reay, R.S., Blodgett, D.W., Burns, B.S., Weber, S.J., and Frey, T. 1990. Management guide for deer wintering areas in Vermont. Department of Forests, Parks and Recreation and Department of Fish and Wildlife, Montpelier, Vermont.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., and Wissmar, R.C. 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* **7**: 433–455.
- Rogers, R.S. 1978. Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and postsettlement history. *Can. J. Bot.* **56**: 843–854.
- Ross, H.H. 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.* **59**: 235–242.
- Sahade, R., Tatian, M., Kowalke, J., Kuehne, S., and Esnal, G.B. 1998. Benthic faunal associations on soft substrates at Potter Cove, King George Island, Antarctica. *Polar Biol.* **19**: 85–91.
- Singh, M.P., Smith, S.M., and Harrison, A.D. 1984. Emergence of some caddisflies (Trichoptera) from a wooded stream in southern Ontario. *Hydrobiologia*, **112**: 223–232.
- Smock, L.A., and MacGregor, C.M. 1988. Impact of the American chestnut blight on aquatic shredding macroinvertebrates. *J. North Am. Benthol. Soc.* **7**: 212–221.
- Sousa, W.P. 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* **15**: 353–392.
- Speiser, R., and Bosakowski, T. 1987. Nest site selection by northern goshawks in northern New Jersey and southeastern New York. *Condor*, **89**: 387–394.
- Stout, B.M., III, Benfield, E.F., and Webster, J.R. 1992. Effects of forest disturbance on shredder production in southern Appalachian headwater streams. *Freshwater Biol.* **29**: 59–69.
- Strahler, A.N. 1964. Quantitative geomorphology of drainage bas-

- ins and channel networks. *In* Handbook of applied hydrology. *Edited by* Ven te Cow. McGraw-Hill, New York. pp. 16–33.
- Sullivan, K., Black, B., Mahan, C., Abrams, M., Kim, K.C., and Yahner, R. 1998. Overstory tree composition of hemlock and hardwood stands in Delaware Water Gap National Recreation Area. Center for Biodiversity Research, Environmental Resources Research Institute, Pennsylvania State University, University Park, PA 16802, U.S.A.
- Wallace, J.B. 1996. Habitat, life history, and behavioral adaptations of aquatic insects. *In* Aquatic insects of North America. *Edited by* R.W. Merritt and K.W. Cummins. Kendall/Hunt Publishing, Dubuque, Iowa. pp. 41–73.
- Wallace, J.B., and Gurtz, M.E. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. *Am. Midl. Nat.* **115**: 25–41.
- Wallace, J.B., Eggert, S.L., Meyer, J.L., and Webster, J.R. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecol. Monogr.* **69**: 409–442.
- Ward, J.V., and Stanford, J.A. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* **27**: 97–117.
- Webster, J.R., and Benfield, E.F. 1986. Vascular plant breakdown in freshwater ecosystems. *Annu. Rev. Ecol. Syst.* **17**: 567–594.
- Webster, J.R., Golladay, S.W., Benfield, E.F., Meyer, J.L., Swank, W.T., and Wallace, J.B. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic laboratory. *In* River conservation and management. *Edited by* P.J. Boon, P. Calow, and G.E. Petts. John Wiley and Sons Limited, West Sussex, England. pp. 231–253.
- Wellnitz, T.A., Radar, R.B., and Ward, J.V. 1996. Importance of light and nutrients in structuring an algal community in a Rocky Mountain stream. *J. Freshwater Ecol.* **11**: 399–413.
- Wilkinson, L. 1998. SYSTAT 8.0 Statistics (user manual). SPSS, Inc., Chicago, Illinois.
- Yamasake, M., DeGraaf, R.M., and Lanier, J.W. 1999. Birds, smaller mammals, and forest carnivores. *In* Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. *Edited by* D.A. McManus, D.S. Shields, and D.R. Souto. U.S. Department of Agriculture, Forest Service, Newton Square, Pa. pp. 135–143.
- Young, J.A., Smith, D.R., Snyder, C.D., and Lemarié, D.P. 2002. A terrain-based paired-site sampling design to assess biodiversity losses from eastern hemlock decline. *Environ. Monit. Assess.* In press.
- Yount, J.D., and Niemi, G.J. 1990. Recovery of lotic communities and ecosystems from disturbance—a narrative review of case studies. *Environ. Manag.* **14**: 547–569.
- Zimmerman, G.M., Goetz, H., and Mielke, P.W., Jr. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology*, **66**: 606–611.