Long-term Effects of Hemlock Forest Decline on Headwater Stream Communities

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ABSTRACT

We conducted a comparative study to determine the potential long-term impacts of hemlock forest decline on fish and benthic macroinvertebrate assemblages in headwater streams in the Delaware Water Gap National Recreation Area. Hemlock forests throughout eastern North America have been declining due to 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 were more diverse but less productive than streams draining mixed hardwood forests. In addition, there were distinct differences in macroinvertebrate trophic structure, with predators more common and grazers less common in hemlock-drained streams. In contrast, forest-type differences in fish assemblage structure were less pronounced, although trends suggested that species richness was higher in streams draining hardwood and functional diversity was higher in hemlock-drained streams. We also found important distinctions in terms of fish species composition. Brook trout (*Salvelinus fontinalis*), an important fishery in the park, were three times more likely to occur and four times more abundant in streams draining hemlock than in those draining hardwood forests. Also, fish trophic structure varied between forest type, with insectivores more common in hardwood-drained streams and piscivores more common in hemlock-drained streams. Analysis of stream habitat data indicated that streams draining hemlock forests had more stable thermal and hydrologic regimes. Our findings suggest hemlock decline may result in long-term changes in headwater stream ecosystems that are comparable in scope to effects observed in terrestrial ecosystems.

KEY WORDS

Ecological effects, aquatic communities, hemlock forest decline, headwater streams, habitat stability.

INTRODUCTION

Eastern hemlock (*Tsuga canadensis*) forests have declined substantially in the last two decades as a result of the hemlock woolly adelgid (*Adelges tsugae*). 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. The importance of hemlock to many terrestrial assemblages has been documented (reviewed in McManus 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 (see Molles 1982, Stout et al. 1992).

There have been numerous reports of significant changes in headwater stream habitat and aquatic 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 inputs 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 assemblages (Wallace and Gurtz 1986, Sheldon 1988). 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 macroinvertebrate and fish 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 assemblages. Since 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 our predictions reflect realistic assumptions regarding long-term changes in forest composition.

METHODS

STUDY AREA

Delaware Water Gap National Recreation Area (DEWA) is located in northeastern Pennsylvania and western New Jersey. The park encompasses 27,742 hectares of forested hills, ravines, and bottom lands straddling the Delaware River. 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 hectares), 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 prior to 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 perma-

nent woodlots with reduced disturbance histories (Foster et al. 1998). 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 more abundant in DEWA in the past.

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 south-eastern portion of the Park. Since this study was conducted, impacts from HWA have increased dramatically (R. Evans, personal communication).

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) that 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 end points 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 prior to comparing aquatic invertebrate community measures between forest types. Ultimately, we selected 14 pairs of watersheds that were similar in terrain (defined by channel slope, aspect, solar radiance, channel shape, and elevation) and stream size but varied in forest species composition. Specifically, one watershed in each pair was comprised mainly of hemlock and the other watershed in each pair was comprised mainly of mixed hardwood species. See Young et al. (2002) for a complete description of the study design and GIS methods used to stratify sampling.

FIELD SAMPLING

Invertebrate sampling was conducted during the early spring of 1997. 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. We took a total of twenty 30-second kick samples with a D-frame kick net at random locations within each stream reach. See Snyder et al. (2002) for a complete description of methods used to collect and process macrinvertebrate samples.

Fish sampling was conducted in July 1997 during base flow conditions. However, because of the abnormally dry summer, 16 of the 28 initially selected streams dried totally. The 12 streams that remained wetted (7 in hemlock and 5 in hardwood) were sampled using a backpack electroshocking unit. Sampling reaches were defined the same as for macroinvertebrates. See Ross et al. (2003) for details regarding fish sampling.

Instream habitat measurements were taken within the same stream reaches used to collect macroinvertebrates and fish. We collected information on water chemistry, flow, water temperature, and stream channel morphology. Water chemistry included dissolved oxygen, pH, specific conductivity, nitrates, nitrites, ammonia nitrogen, total phosphates, and orthophosphates. Flow was measured during spring high-flow conditions and temperature was measured every hour with Optic StowAway™ temperature loggers. Stream channel measurements included 1) microhabitat diversity, 2) large woody debris (LWD), and 3) the extent to which each stream dried during the summer. See Snyder et al. (2002) for detailed descriptions of instream habitat sampling methods.

STATISTICAL ANALYSES

We compared four measures of invertebrate assemblage structure between streams draining hemlock and hardwood forests: taxa richness, Simpson's evenness index, total density, and 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 difference in each community structure metric between site pairs was 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 a paired t-test to test the statistical significance of the effect of forest type on each measure.

Likewise, we compared three measures of fish assemblage structure between hemlock- and hardwood-drained streams: species richness, species diversity (Shannon-Weiner), and trophic diversity (Ross et al. 2003). However, for fish, we were unable to use the paired site approach to test for differences in community structure because over half of the 28 selected sites dried up prior to fish sampling. Instead, we used a 3-way ANOVA to assess effects of terrain, stream size, and forest type and their interactions on the three fish community structure metrics.

We also compared the taxonomic and trophic composition of both fish and 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. For trophic composition, we used multi-response permutation procedure (MRPP) to analyze forest-type effect on the proportion of individuals in multiple trophic groups. For invertebrates there were four groups (shredder-detritivores, collector-detritivores, grazer-algivores, and predators) and for fish there were three groups (piscivore, insectivore, and omnivore). MRPP is a non-parametric 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).

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. We used an alpha value of $P = 0.10$ for all tests of significance.

RESULTS

AQUATIC COMMUNITY STRUCTURE

From the 28 sites, we collected a total of 53,868 invertebrates from 151 taxa. The number of invertebrate 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 zero and 10. Total density ranged between 116 - 4698 individuals $\cdot$ m^{-2}. In terms of fish, we collected a total of 1,406 individuals from 15 species and seven families. However, fish sampling was limited to the 12 sites that remained wetted when sampling occurred in July. Most sites harbored between one and four fish species though we collected 12 species from one site.

Despite large variances observed within forest types, we found statistically significant differences in all four invertebrate assemblage response variables. Streams draining hemlock supported on average about 1.5 times more total invertebrate taxa (mean difference = 14 taxa) and 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 $\cdot$ m^{-2}) and supported more rare taxa (mean difference = 2 taxa) than streams draining hemlock (Figure 1).

In contrast, none of the three fish assemblage structure measures were significantly different between forest types (ANOVA, $p > 0.25$) although the reduced sample sizes compromised our power to detect differences considerably. Trends suggest that species richness may have been higher in mixed hardwood sites and functional diversity may have been higher in hemlock sites (Figure 2).

Results of odds ratio tests for each invertebrate taxa indicated that forest-specific differences in taxa richness were associated with specific taxa and not simply a random subset of the community. Eleven taxa (7.3% of total) showed strong associations with hemlock (Odds ratio test, $p < 0.10$) while no taxa were strongly associated with hardwood forests (Figure 3). 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. Of the 28 taxa that showed either strong or weak associations with hemlock, three were found to occur exclusively in hemlock-dominated watersheds while no taxa were found to occur only in streams draining hardwood forests (Figure 3).

Results of odds ratio tests indicated that occurrence patterns were not significantly different for any of the 11 fish taxa. However, again, statistical power was poor because of reduced sample size. Two species showed forest-specific trends. Bluegill (*Lepomis*

machrochirus) was found more often in streams draining hardwood forests (14% of hemlock sites compared to 60% of hardwood sites), whereas, brook trout (*Salvelinus fontinalis*) was found more often in streams draining hemlock forest (57% of hemlock sites compared to 20% of mixed hardwood sites).

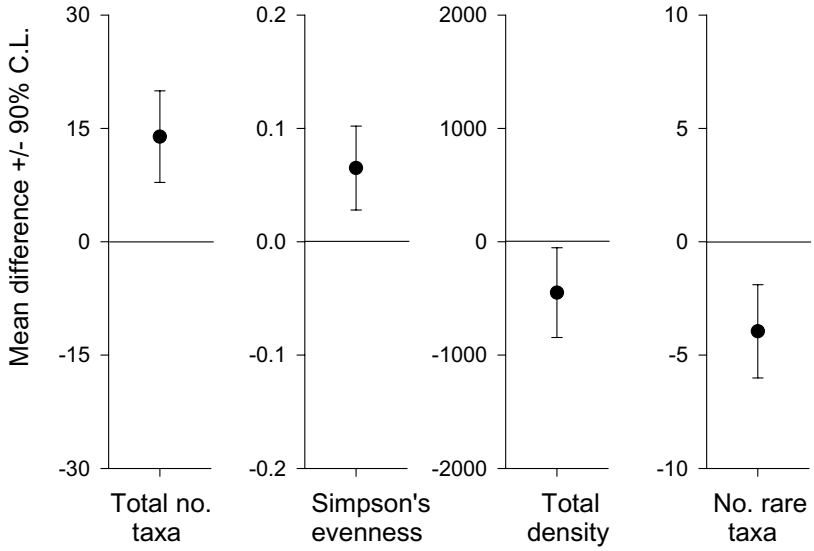

Figure 1. Average difference (± 90% CL) in four aquatic macroinvertebrate assemblage metrics between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Cases where 90% confidence limits do not overlap 0 indicates statistical significance (p<0.10).

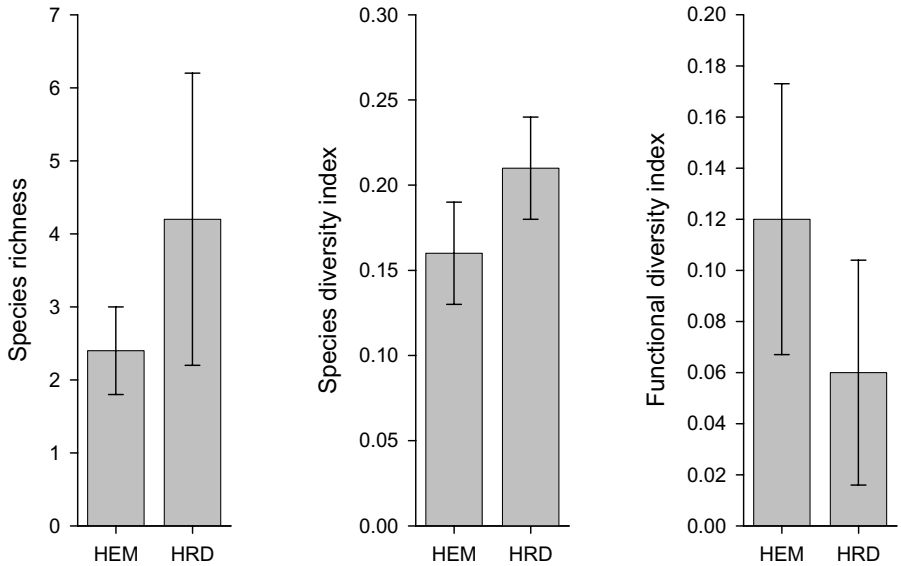

Figure 2. Comparison of three fish assemblage structure metrics between streams draining hemlock and streams draining hardwood forests. Graphs show means ± SE.

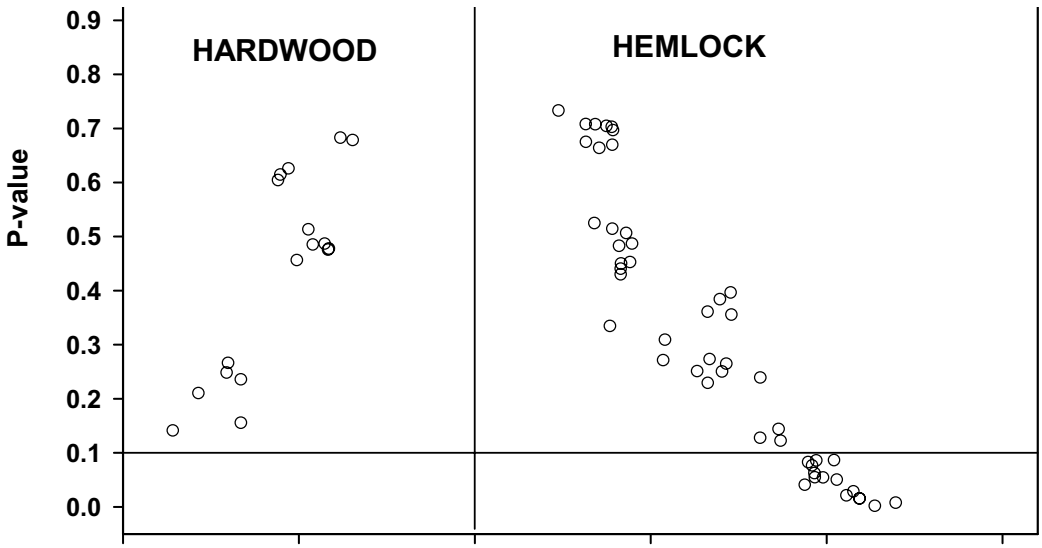

Figure 3. Results of odds ratio test to determine taxa-specific associations with vegetation types. For each taxa, ratio of occurrence in streams draining hemlock to that draining hardwood was used, and therefore, positive values indicate a preference for hemlock. Figure 3 shows the significance as a function of the odds ratio. Species with p-values less than 0.1 were deemed strong associates and those with values between 1.0 and 0.3 were deemed weak associates.

Trophic composition of invertebrate assemblages (i.e., the proportion of individuals in each of the four trophic groups) also differed between streams draining hemlock and hardwood forests (ä = 2.18; p = 0.009). Predators comprised a significantly larger fraction and grazer-algivores a significantly smaller fraction of the invertebrate assemblage in hemlock-drained streams (Figure 4). The proportion of individuals as shredders and collectors did not differ between forest types.

We also observed forest-specific differences in trophic composition for fish (Figure 5). On average, insectivores comprised a significantly larger fraction of the fish community in mixed hardwood sites (mean proportion = 0.77) than in hemlock sites (mean = 0.34) (ANOVA, F = 3.39, p = 0.09), whereas piscivores were proportionally more abundant in hemlock sites (mean = 0.61) than in hardwood sites (mean = 0.21) (ANOVA, F = 2.36, p = 0.15).

STREAM HABITAT

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

Median daily stream temperatures at hemlock sites tended to be cooler in the summer, warmer in the winter, and less variable throughout the year. Perhaps even more important to the species that inhabit these streams are the extremes in temperatures in which they are exposed. In particular, we found that summer daily maxima were lower and summer daily minima were higher in hemlock-drained streams. For example, summer daily maxima in streams draining hardwood forests exceeded 20°C over 18% of the time compared to less

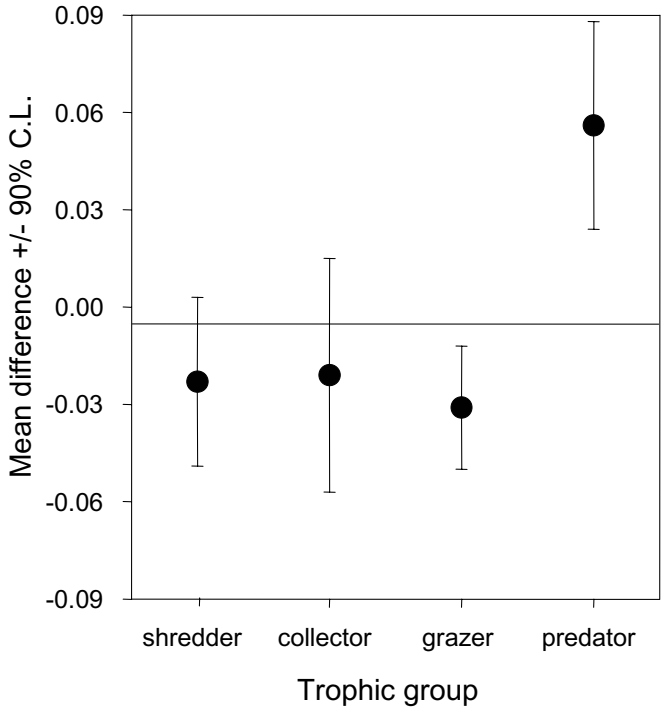

Figure 4. Comparisons of mean differences (± 90% CL) in macroinvertebrate trophic composition between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock.

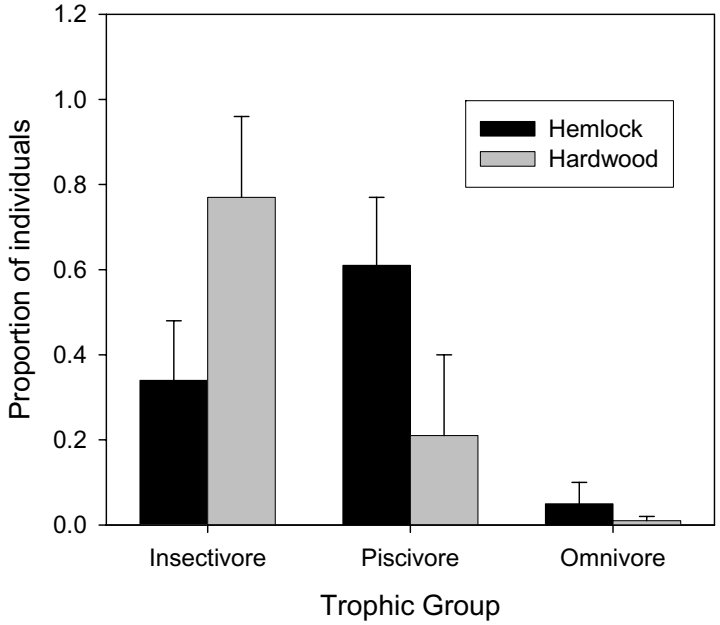

Figure 5. Comparisons of fish trophic composition between steams draining hemlock and hardwood forests. Graph shows mean proportions ± SE.

than 3% of the time in streams draining hemlock, and minimum daily temperatures dropped below freezing 8% of the time in hardwood sites compared to only 0.2% of the time in hemlock sites (Figure 6).

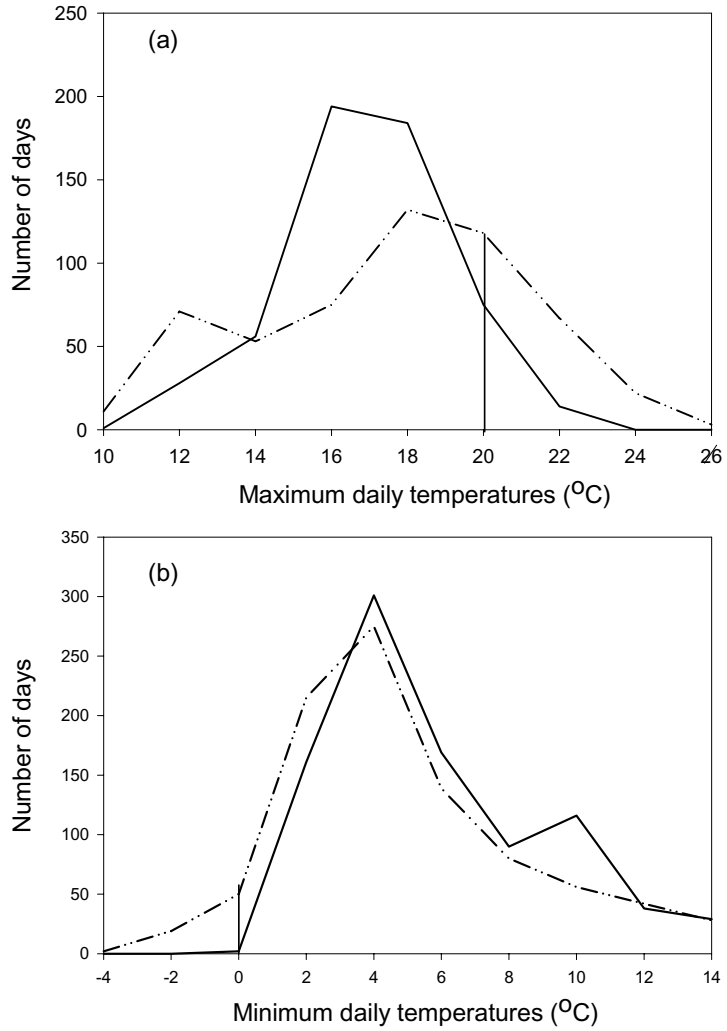

Figure 6. Comparisons of the distributions of (a) summer (July-September) maximum temperatures and (b) winter (October-February) minimum temperatures between streams draining hemlock and hardwood forests. Solid lines represent hemlock forests and dashed lines represent hardwood forests. Vertical lines represent arbitrary thresholds for comparison.

We used flow data from the USGS 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 (see Table 1). Specifically, over the 90-year period between 1908 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, nine out of 14 (64%) of streams draining hardwood

forests became dry or mostly dry, while two out of 14 (14%) of streams draining hemlock dried partially. None of the streams draining hemlock dried completely compared with four out of 14 (29%) of the 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 six out of 14 (43%) of streams draining hardwood dried completely, compared to only one out of 14 (7%) of the streams draining hemlock (R. Evans, personal communication).

Table 1. Qualitative assessments of drying for all 28 streams (14 hardwood and 14 hemlock) taken in July 1997, during a period of prolonged drought. Drying classes were based on the proportion of stream channel that remained wetted. The table shows the number of streams (percentage of total in parentheses) for each forest type.

Drying Class	Hemlock	Hardwood
Dry (0%)	0 (0%)	4 (29%)
Mostly dry (<50%)	2 (14%)	5 (36%)
Mostly wet (>50%)	3 (21%)	0 (0%)
Wet (100%)	9 (64%)	5 (36%)

DISCUSSION

After accounting for differences in terrain and stream order, we found aquatic invertebrate community structure was significantly different between streams draining hemlock and mixed hardwood forests. Streams draining hemlock forests supported more total taxa than streams draining hardwood forests, and over 7% of the taxa showed strong associations with hemlock, including three taxa that were 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.

In contrast, forest-specific differences in fish assemblage structure were not as pronounced although there was some evidence (though weak) that species richness was higher in streams draining mixed hardwood and functional diversity was higher in hemlock-drained streams. We also observed weak associations between two fish species and forest type: brook trout were more likely to occur and more abundant in hemlock-drained streams than hardwood and blue gill were more likely to occur in mixed hardwood drained streams. Statistical associations may have been weaker for fish because of the lower sample size. However, it is also possible that the status of fish species and assemblages are less directly associated with forests surrounding streams because they are able to move in and out of streams. In this case, synoptic information on occurrence patterns may not be definitive because individuals may visit

(e.g. for foraging) suboptimal habitats but still require other habitats to complete their life cycles and persist in the longer term. For example, summer stream temperatures may be too warm in streams draining mixed hardwood to support brook trout breeding but individual trout may frequently forage in hardwood-drained streams. If so, over time, widespread hemlock decline would likely have a significant impact on trout populations. In this case, a more intensive research effort would be required that evaluated fish movement patterns and time spent in various habitats in order to determine forest type effects.

We observed differences in stream habitat that could explain differences in benthic macroinvertebrate diversity and fish species composition 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 sub-zero temperatures observed in hardwood-drained streams could promote the formation of anchor ice, which has been found to a major factor regulating benthic assemblages by reducing taxa richness and limiting reproductive habitat (Miller and Stout 1989). Moreover, more stable thermal regimes may help minimize exposure of fish and benthic communities to temperatures outside the optimum range for many component species. More moderate thermal regimes would likely have positive effects on both invertebrates and fish, but may be particularly important in explaining higher brook trout occurrence and abundance patterns in streams draining hemlock. Specifically, brook trout prefer stream temperatures of 14-16°C and spawning is virtually restricted to water of 15°C and below. Furthermore, the upper lethal limit of hatchlings is 20°C, and adults are rarely found in streams where summer temperatures exceed 21°C (Jenkins and Burkhead 1993). The fact that summer maxima exceeded 20°C over 17% of the time in streams draining hardwood forests compared with 3% of the time in streams draining hemlock strongly supports the conclusion that a hemlock-induced effect on moderating stream temperatures was responsible for the distribution and abundance patterns of brook trout that we found. Likewise, there is evidence that benthic assemblages in headwater streams are more diverse in cooler, more thermally static streams (Kamler 1965).

Greater stability of summer baseflows 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. There is little doubt that stable base flows would afford, at least, short-term benefits to stream invertebrate communities. Since most aquatic insect species require at least one year to complete their life cycles (Wallace 1996), stream drying would likely kill or displace a large fraction of the benthic community leading to lower densities and diversity. Although disturbances such as floods and droughts may have positive effects on diversity patterns in the longer term (e,g., Resh et al. 1988), 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 associated 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 (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 (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 due to 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 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, and notable differences in fish assemblages, though fish results are less clear. Further, our results suggest that forest-type differences in light and temperature regimes, stability of summer baseflows, 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 assemblages including a reduction in invertebrate diversity, a change in fish and invertebrate trophic structure, and possibly a decline in brook trout populations. Concern over trout fisheries may be even more pronounced in more southern areas where hemlock may be even more important in maintaining cooler summer temperatures required by trout.

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 field work. Funding for the research was obtained through the National Park Service's Natural Resources Preservation Program (NRPP).

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