

POTENTIAL IMPACTS OF HEMLOCK WOOLLY ADELGID

(*Adelges tsugae*) ON EASTERN HEMLOCK

(*Tsuga canadensis*) ECOSYSTEMS

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ABSTRACT

Eastern hemlock, an extremely shade tolerant, late successional ("climax") conifer with a dense, evergreen crown and an extensive, shallow, root network, strongly influences its environment and other species. Dense hemlock canopies create distinctive microclimates and an acidic "duff" layer. The characteristically dark, acidic conditions below dense hemlock canopies can alter fundamental community and ecosystem characteristics such as plant and animal species composition, succession dynamics, primary productivity, decomposition, and nutrient cycling. At a landscape scale, hemlock-dominated evergreen "patches" add diversity to the predominantly deciduous "matrix" of the eastern forest. Within mixed hardwood stands, scattered hemlock trees provide unique evergreen habitat structure. A number of bird species are strongly associated with hemlock throughout their ranges, or portions thereof. In New England, hemlock provides important winter wildlife shelter. Further south, hemlock probably helps provide summer habitat for cold water fish such as brook trout (*Salvelinus fontinalis*), by shading and cooling streams.

The National Park Service sponsored studies of hemlock woolly adelgid (HWA) and hemlock health, understory vegetation, breeding song birds, small mammals, amphibians, terrestrial invertebrates, and environmental conditions such as light and temperature regimes, in two hemlock ravines at Delaware Water Gap National Recreation Area. Studies in these hemlock ravines have documented more than 300 plant species, including approximately 120 bryophyte species (moss and liverwort); 12 small mammal species (7 rodent, 5 soricid); 15 amphibian species (9 salamander, 4 frog, 2 toad); and 22 breeding song-bird species. Breeding populations of several bird species strongly associated with hemlock, including blackburnian warbler (*Dendroica fusca*), black-throated green warbler (*Dendroica virens*) and solitary vireo (*Vireo solitarius*), were estimated. Occurrences of several regionally rare species of plants and small mammals were documented. Stream temperature studies indicated that the cooling effect of the hemlock ravine was essential to maintain temperatures tolerable to brook trout.

The potential impacts of HWA infestations on ecosystems must be considered within a context of broader environmental and historical changes. The prevalence of hemlock throughout eastern forests has been dramatically reduced from what it was in presettlement times (prior to 1750). Currently, interactions among myriad potential forest stressors and disturbances -- including acidic deposition and ozone, elevated herbivore (deer) populations, and invasions of numerous exotic forest insects, diseases, plants, and animals -- may strongly influence not only the susceptibility and response of hemlock trees to HWA infestations, but also the ecosystem response to hemlock defoliation and mortality. Expected impacts include the following: reduced populations of birds associated strongly with hemlock; increased understory and stream light levels and temperatures; reduced populations of native brook trout, and possibly increased populations of non-native brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*); reduced biomass and species diversity of bryophytes; increased soil nitrate-nitrogen availability; increased primary productivity; increased deciduous leaf litter input to streams; increased biomass of understory plants (e.g. ferns) and stream algae; increased occurrences of invasive exotic plants, such as Japanese stilt-grass (*Microstegium vimineum*); and gap colonization and capture by "middle -successional" tree species, such as yellow birch (*Betula alleghaniensis*) and red maple (*Acer rubrum*).

INTRODUCTION

The effects of hemlock woolly adelgid (HWA) on eastern hemlock ecosystems should be considered not in isolation, but within a context of broader environmental and historical changes. Before eastern forests were cleared by European colonists (circa 1750-1850), hemlock dominated much more extensive areas than it does today (Foster and Zebryk 1993, Whitney 1990, McIntosh 1972). In Wisconsin and Michigan, only 0.5% of presettlement hemlock remains (Mladenoff 1995, White and Mladenoff 1994). In Pennsylvania, vast areas of

hemlock were cut for use in the tanning industry during the late nineteenth and early twentieth centuries (Quimby 1996, Whitney 1990). Recent unsuccessful hemlock regeneration has been attributed, at least in part, to browsing by white-tail deer (*Odocoileus virginianus*) (Whitney 1990, Anderson and Loucks 1977, Hough 1965). As a late successional or "climax" species, hemlock forests require hundreds of years without major environmental disturbances to mature (Foster and Zebryk 1993, Tyrrell and Crow 1994). But it is clear that we are living in an era of increasing environmental stressors or "disturbances," such as air and water pollution (e.g. ozone, acidic deposition), habitat fragmentation, climate changes, elevated herbivore (deer) populations, and invasions of numerous other exotic forest insects, diseases, plants, and animals. Invasive exotic species can alter fundamental characteristics and processes of ecosystems, such as light and temperature regimes, primary productivity, and nutrient cycling, and thus change the "fundamental rules of existence" for all organisms within affected ecosystems (Vitousek 1990).

Gypsy moth (*Lymantria dispar*), Dutch elm disease (*Ophiostoma ulmi*), beech bark disease (*Nectria coccinea* and *N. galligena*), and white pine blister rust (*Cronartium ribicola*) are just a few examples of other exotic species that also affect the health and composition of eastern forests (Miller-Weeks et al. 1994). Hemlock defoliation and mortality provides opportunities for exotic plants such as tree of heaven (*Ailanthus altissima*), Japanese barberry (*Berberis thunbergii*), and Japanese stilt-grass (*Microstegium vimineum*) to invade and further disrupt forest ecosystems. Japanese stilt-grass has invaded at least one HWA-impacted hemlock stand in Connecticut (Lapin 1994). The numerous "agents of environmental change" affecting eastern forests diminish the likelihood that healthy, mature hemlock stands will persist long into the future. The interactions of all these "agents" also diminish the likelihood of successfully predicting the ecosystem effects of HWA infestations.

To identify the potential impacts of HWA on hemlock ecosystems, knowledge of two subjects is required: (1) the effects of HWA on hemlock trees, and (2) the ecosystem consequences of those effects. While it is clear that HWA represents a serious threat to eastern hemlocks (McClure 1991), research is needed to fill critical gaps in knowledge of both subjects. HWA has been closely associated with extensive, severe hemlock defoliation and mortality in Connecticut (McClure 1991), Virginia (Shenandoah National Park; Watson 1992), New Jersey (Ward et al. 1992), and other areas. The hemlock defoliation and mortality experienced in these areas have not occurred in hemlock stands free of HWA. However, these two lines of evidence do not force us to conclude that severe hemlock defoliation and mortality will occur within a specified number of years at all sites having HWA infestations. It is possible that the effects of HWA on hemlock trees vary geographically, depending on environmental site or stress factors and the genetics of particular HWA and hemlock populations. Environmental site or stress factors include: elevation, slope, aspect, soil moisture, and other characteristics; pollutants such as acidic deposition, ozone, and road salt; forest

age and species composition; presence of "generalist" forest-defoliating insects such as gypsy moth (*L. dispar*) and fall cankerworm (*Alsophila pometaria*), as well as "specialist" hemlock feeding insects such as hemlock loopers (*Lambdina fiscellaria* and *L. athasaria*), scales (*Fiorinia externa* and *Nuculaspis tsugae*), and borers (*Melanophilafulvoguttata*). Interactions among these factors may strongly influence the susceptibility and response of hemlock trees to HWA infestations.

Studies documenting the effects of HWA on hemlock ecosystems have not been completed. Such studies were initiated in 1993 by the National Park Service at Delaware Water Gap National Recreation Area, and are continuing. These studies are providing important "baseline" information about hemlock ecosystems, but have not yet documented ecosystem effects of HWA, since the hemlocks from the study area have not been significantly affected by HWA to date.

In the absence of completed ecological studies (and with assumptions about the rate and manner of hemlock defoliation and mortality caused by HWA), we can use two approaches to identify potential ecological impacts. First, we can use knowledge of the ecological roles of existing hemlocks, and the mechanisms of ecological interactions, to reach logical predictions about HWA impacts. Second, we can assume the ecological impacts of HWA will be "similar" to those of some other type of forest disturbance that has been studied, such as other forest insect defoliators, or tree gap dynamics. We use both approaches in this discussion, and present some results from the hemlock ecosystem studies conducted at Delaware Water Gap National Recreation Area. Lapin (1994) discussed potential impacts of HWA on resources in the lower Connecticut River valley.

OVERVIEW OF ECOLOGICAL RELATIONSHIPS INVOLVING HEMLOCK

Eastern hemlock is currently distributed from the maritime provinces of eastern Canada, west to Minnesota, south through Ohio, and along the Appalachian Mountains to the northern edge of Georgia and Alabama. On the existing, postsettlement landscape, hemlock is most typically dominant on cool, mesic sites with nutrient-poor soils (Rogers 1978). Hemlock requires a moist, temperate climate, and is susceptible to heat and drought stress (Quimby 1996, Secrest et al. 1941, Stickel 1933). Hemlock is generally more abundant and evenly distributed across the landscape in the northeastern part of its range than in the southern and western parts of its range, where it becomes increasingly restricted to isolated stands inhabiting moist cool valleys, steep ravines, coves, and north-facing bluffs (Eyre 1980, Keever 1973). Benzinger (1994a) provided an excellent review of hemlock ecology.

Eastern hemlock, an extremely shade tolerant, late successional ("climax") conifer with a dense, evergreen crown and an extensive, shallow root network, can strongly influence the surrounding environment and other species.

Research has documented a number of these influences, but additional research is needed to answer important questions and test hypotheses. At a landscape scale, "patches" of evergreen hemlock add diversity to the predominantly deciduous "matrix" of the eastern forest. Dense hemlock canopies intercept solar radiation, precipitation, and wind throughout the year, and can thus alter light, temperature, and moisture regimes, and create distinctive microclimates. During summer, many hemlock stands seem darker, cooler, and more humid than nearby hardwood stands. During winter, a hemlock canopy provides shelter from cold winds, and may retain radiant heat on exceptionally clear, cold nights. Research is needed to document such microclimates, and determine the extent to which hemlocks actually cause them, as opposed to merely responding to microclimates caused by other site conditions. Hemlock needles acidify the surrounding soil and create a distinctive "duff" layer.

The year-round shading and characteristically acidic conditions below dense hemlock canopies can alter fundamental community and ecosystem characteristics such as plant and animal species composition, succession dynamics, understory primary productivity, decomposition, and nutrient cycling. Mladenoff (1987) quantified the effects of hemlock stands on nitrogen mineralization (an example of nutrient cycling) and related processes by comparing these processes under intact hemlock canopies with those in treefall gaps and under sugar maple canopies. Increased hemlock canopy cover was correlated with increased soil acidity and decreased nitrification; as hemlock importance approached 50%, nitrification approached zero. Nitrification was more than double under gaps and under sugar maples than it was under hemlocks. Air, litter, and soil temperatures under the hemlock canopy were much lower than in gaps, and somewhat lower than under sugar maple canopies (particularly in spring, before leaf-out).

The ecological influences of a particular hemlock stand depend upon its size, shape, geographic location, species composition, and the size and age structure of its trees. Scattered hemlock trees within mixed hardwood forests typically retain their lower branches, and so provide unique evergreen habitat structure extending nearly from the forest floor to the upper canopy. Clearly, the ecosystem effects of a very small, sparse stand of young hemlocks will be very different from those of a very large, pure, "old growth" stand. Even among old growth stands, important differences exist. Tyrrell and Crow (1994) documented significant differences in structural characteristics (such as tree density, basal area of snags, volume of fallen logs, percent canopy area with open gaps, and sizes of individual canopy gaps) among hemlock stands in northern Wisconsin and the Upper Peninsula of Michigan ranging in age from about 175 to 375 years old. Structural characteristics of hemlock stands greater than 300 years old were distinctly different than those of stands less than 275 years old in their study. Thus, the structural and ecological characteristics of hemlock stands continue to change and develop for upwards of 300 years after original establishment.

The ecological roles of structurally similar hemlock stands can also be expected to vary over geographic regions. For example, hemlock does not seem to play as critical a role as winter shelter for wildlife (e.g. "deer yards") in the South as it does in New England. Conversely, hemlock probably plays a more critical role in the South than it does in New England for maintaining the cool summer stream temperatures required by native brook trout. Hemlock can play different ecological roles even within more restricted geographic areas. In northern Wisconsin, black-throated green warblers (*Dendroica virens*), blackburnian warblers (*Dendroica fusca*), and solitary vireos (*Vireo solitarius*) are strongly associated with mature hemlock stands, but in southern Wisconsin, magnolia warblers (*Dendroica magnolia*) and Canada warblers (*Wilsonia canadensis*) are hemlock associates (Howe and Mossman 1995). DeGraff et al. (1992) and DeGraff and Rudis (1986) provide much information about relationships of hemlock with wildlife species in New England.

HEMLOCK ECOSYSTEM AND BIODIVERSITY STUDIES AT DELAWARE WATER GAP NATIONAL RECREATION AREA

Delaware Water Gap National Recreation Area encompasses 70,000 acres along the northeastern edge of Pennsylvania and the northwestern edge of New Jersey, and surrounds the "Middle Delaware National Scenic and Recreational River" (a 40-mile-long segment of the Delaware River). The National Park Service initiated studies in two hemlock ravines within the recreation area during 1993 to provide basic information regarding (1) HWA infestations, (2) hemlock tree health, and (3) hemlock ravine biodiversity and ecosystem characteristics. We established a system of 60 permanent hemlock plots in the two hemlock ravines to monitor HWA infestation levels and hemlock tree health. We collected data from these plots during the past three years (1993-1995) using standardized USDA Forest Service protocols. Onken (1996) analyzed and summarized these data. We documented locations of the permanent hemlock plots with a global positioning system (GPS). HWA was first detected in one of the study ravines during 1994, and in the other ravine during 1995. Ecological studies in these two hemlock ravines have included small mammals, amphibians, terrestrial arthropods, understory vegetation, breeding birds, fish, and environmental conditions such as light and temperature regimes. These studies are summarized below. Results from other published studies are also presented for comparison.

Vegetation

The National Park Service contracted Cornell University to complete a quantitative survey of understory vegetation, including bryophytes, in the two hemlock ravines. A total of 92 understory vegetation plots were established; 60 of these were located in the center of the 60 permanent hemlock plots in the two study areas. Data were collected at each plot regarding the species composition

and abundance of overstory trees, tree seedlings and saplings, ferns, flowering herbs, and bryophytes. At each plot, the percent of total available light reaching the understory vegetation throughout the growing season was calculated, and expressed as a "gap light index" (GLI). In addition, data were collected regarding slope, aspect, soil depth, temperature, and moisture at each plot. Multivariate statistical analyses (TWINSPAN and Canonical Correspondence Analysis) were used to detect patterns of species abundance in relation to each other and to the measured environmental variables. Statistical power analyses were completed to determine the minimum amount of change in plant populations that could be confidently detected. Finally, qualitative surveys of the vegetation in the two ravines were completed to identify species that did not occur within the permanent plots.

As is characteristic of understory vegetation in hemlock-dominated stands, vegetation in the study ravines was sparse, and concentrated in "patches." Yet, more than 300 plant species were identified, including 44 species of trees or shrubs, 26 species of ferns or fern-allies, 108 species of flowering herbs, and more than 120 species of bryophytes. Eastern hemlock comprised over 50% of the basal area of both study areas. Other prominent canopy trees included yellow birch (*Betula alleghaniensis*), sweet birch (*B. lenta*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), white oak (*Quercus alba*), and white pine (*Pinus strobus*).

Multivariate analyses indicated that vegetated areas within the ravines tended to be dominated by one of four groups: ferns, shade-tolerant herbs, tree seedlings, or bryophytes. Light availability (GLI) and soil moisture were the environmental variables exerting the most control over species distributions within the ravines. Dominant ferns were intermediate wood fern (*Dryopteris intermedia*), New York fern (*Thelypteris noveboracensis*), and hayscented fern (*Dennstaedtia punctilobula*). The most common tree seedlings were birches, sugar maple, and red maple. The most common flowering herbs were partridgeberry (*Mitchella repens*), Indian pipe (*Monotropa uniflora*), Northern white violet (*Viola pallens*), white wood aster (*Aster divaricatus*), Canada mayflower (or wild lily-of-the-valley (*Maianthemum canadensis*), and sessile bellwort (or wild oats, *Uvularia sessilifolia*). Several flowering herb species listed as threatened or endangered in Pennsylvania or New Jersey were present, such as white twisted stalk (*Streptopus amplexifolius*), checkered rattlesnake plantain (*Goodyera tessellata*), and long beech fern (*Thelypteris phagopteris*).

Amphibians, Small Mammals, and Terrestrial Arthropods

The National Park Service funded and assisted the New Jersey Division of Fish, Game, and Wildlife to complete a quantitative study of small mammals and amphibians using pit-fall and snap traps in both hemlock ravines. In each ravine, 36 trap arrays were established (locations documented with GPS

technology) over an area of approximately 11 hectares. Numerous habitat characteristics in the vicinity of each trap were measured. Traps were "activated" for ten continuous days in August 1993 and August 1994, and terrestrial arthropods captured in the pit-fall traps were preserved for identification.

A total of 12 small mammal species (7 rodent, 5 soricid) and 15 amphibian species (9 salamander, 4 frog, 2 toad) were collected from the two hemlock ravines. The four most abundant small mammals captured were smokey shrews (*Sorex fumeus*), white-footed mice (*Peromyscus leucopus*), masked shrews (*Sorex cinereus*) and red-backed voles (*Clethrionomys gapperi*). A Northern water shrew (*Sorex palustris*), which is rare in Pennsylvania, was captured for the first time in New Jersey, and pygmy shrews (*Sorex hoyi*) were captured for only the second time in New Jersey. The four most abundant amphibians collected were red-backed salamanders (*Plethodon cinereus*), red-spotted newts (*Notophthalmus viridescens*), American toads (*Bufo americanus*), and slimy salamanders (*Plethodon glutinosus*).

Both hemlock ravines apparently supported a relatively high number of small mammal species, and also a high total small mammal population density, in comparison to other forested habitats in Pennsylvania and New Jersey. In a two-year study methodologically comparable to ours (pit-fall and snap traps), but in two mixed deciduous forest sites (primarily maple and oak), Yahner and Smith (1991) captured only eight small mammal species. Dowler et al. (1985) captured only seven small mammal species, and Kirkland and Sheppard (1990) captured only nine small mammal species, even though both these studies included many different sites and habitats. Small mammal abundance, as indicated by the number of animals captured per 100 pit-fall "trap nights," was also high in our hemlock ravine study (20) compared to values found in other habitats in the studies cited above (maximum of 13) .

We have not yet compared the abundance and species richness of amphibians we found in the hemlock ravines to those found in studies of other habitats. The 15 species of amphibians we captured with pit-fall traps is a conservative, minimum estimate of the species present in the hemlock ravines, since many species (such as tree frogs) are not vulnerable to capture by this method. Amphibians seemed to be quite abundant in the hemlock ravines, as indicated by a capture rate of 36 individuals per 100 trap-nights. The generalization that hemlock ravines are "rather sterile as amphibian habitat" (Lapin 1994) may be more appropriately considered an hypothesis (or local condition) than confirmed truth.

Birds

Surveys of breeding song birds were conducted in the two hemlock ravines from late May to early July in 1994 and 1995. A modification of the point count method

described by Ralph et al. (1993) was followed. Species were identified by song. The relative abundance (number of individuals per ten sample points) of each species was estimated, and the probability of detecting a 50% or greater change in selected species populations was calculated.

Twenty-two breeding bird species were documented. Of these, three species that breed primarily within hemlock ravines were relatively abundant: blackburnian warbler (*Dendroica fusca*), 4/10 points; black-throated green warbler (*Dendroica virens*), 8/10 points; and solitary vireo (*Vireo solitarius*), 4/10 points. The blackburnian warbler is associated with eastern hemlock throughout its range, and was once known as the "hemlock warbler." These are "northern" bird species which, in Pennsylvania, breed mainly within the Appalachian Plateau Province, and are associated with large, high-elevation, coniferous forests (Brauning 1992). Hemlock ravines provide the most suitable breeding habitat for these species within the Appalachian Valley and Ridge Province of the recreation area.

Benzinger (1994) provided an excellent review and discussion about the importance of eastern hemlock to breeding birds in New Jersey. He listed the black-throated green warbler, solitary vireo, and Northern Goshawk (*Accipiter gentilis*) as species that, within New Jersey, are found almost exclusively in hemlocks. He listed the Acadian flycatcher, winter wren, hermit thrush (*Catharus guttatus*), red-shouldered hawk (*Buteo lineatus*), and barred owl (*Strix varia*) as species that are usually found in hemlocks. He included the blackburnian warbler, magnolia warbler (*Dendroica magnolia*), red-breasted nuthatch (*Sitta canadensis*), and Cooper's hawk (*Accipiter cooperii*) as species often found in hemlocks, but that are also often found in some other habitat. Howe and Mossman (1995) found the blackburnian warbler, black-throated green warbler, and solitary vireo strongly tied to hemlock forests in Wisconsin and Upper Michigan. The highest population densities of black-throated green warbler, blackburnian warbler, and winter wren were found in mature hemlock forests in this study. Howe and Mossman (1995) also found higher bird diversity in uneven aged, mixed hemlock-hardwood stands than in even-aged, or pure hardwood, stands.

Stream Temperatures and Fish

In the region surrounding Delaware Water Gap National Recreation Area, naturally reproducing populations of native brook trout are closely associated with hemlock stands. Probably the single most important reason for this association is that brook trout need cold water (in summer), and most cold-water streams in this area are surrounded by hemlock stands. Brook trout are generally excluded from streams in which the mean July temperature exceeds 21deg. C (Flebbe 1994). Brook trout survive and grow best at water temperatures between 10°C and 20°C (about 50°F and 68°F), and are severely stressed at water temperatures above

24°C (75°F) (Raleigh 1982). Water temperatures of many streams in the recreation area, even those surrounded by hemlock stands, can exceed 20°C for prolonged periods during summer, and thus can stress brook trout. Both brook trout and brown trout inhabit the two study streams (Ross and Bennett 1996).

We installed computerized electronic temperature recorders at the upper and lower ends of one of the hemlock ravine streams to determine if stream temperatures were consistently lower at the lower end of the ravine than at the upper end. Temperatures were recorded every one-half hour from June to November, 1995. Results revealed that maximum daily summer stream temperatures at the lower end of the ravine were consistently 3°C to 4°C (5.4°F to 7.2°F) cooler than at the upper end (Fig. 1). While stream temperatures at the lower end of the ravine reached levels somewhat stressful to brook trout (21°C), stream temperatures at the upper end reached extremely stressful, and perhaps lethal, levels (exceeding 25°C). The cooling effect of the ravine was essential to maintaining stream temperatures brook trout could tolerate. The cooler water at the lower end of the ravine could be caused by three factors: (1) shade produced by the dense tree (especially hemlock) canopy, (2) shade and "cold air basin" effects produced by the topography (steep slopes, etc.), and (3) cold water input (ground water, tributaries).

To find out if the cooler stream temperatures at the lower end of the hemlock ravine could have been caused by particular "point sources" of cold water input, we measured temperatures every 150 m along the length of the stream on 13 and 18 July, 1995. Two very small tributaries (one intermittent) contributed some cold (17°C) water to the stream, but the stream was not measurably cooler below the confluence of either tributary. Temperatures decreased gradually as the stream passed through the hemlock ravine, from 24°C at the upper end, to 18°C at the lower end.

ECOSYSTEM RESPONSES TO HWA

Disturbance Caused by HWA, and Vegetation Responses

HWA-induced defoliation and mortality of eastern hemlock is qualitatively and quantitatively different from catastrophic disturbances such as clear-cutting, fire, or large-scale wind-throws. It is also different from selectively cutting hemlock. Hemlock defoliation is expected to progress gradually over a period exceeding four years, and dead trees will remain standing for additional periods of time. Understory vegetation and soils will not be violently disturbed by immediate tree falls, and declining hemlock trees will continue to "buffer" the sub-canopy environment to some extent by intercepting light, precipitation, and wind. Forest floor resources previously monopolized and influenced by hemlock (e.g. light, soil moisture, nutrients) will gradually become available to other plants. In particular, more nitrate nitrogen and phosphorus will be available to plants

(Mladenoff 1987). Sub-canopy growing season temperatures will be higher. In response, understory plants such as ferns and tree seedlings (e.g. yellow birch, black birch, red maple), and sub-canopy trees (yellow birch, red maple, white pine) will grow and expand to "fill the gap." Understory species composition will change more or less dramatically. In particular, many bryophyte species may be eliminated. Affected stands will appear to be a "mess," with many dead and dying hemlock trees, openings in the canopy, and apparent "weedy" growth. Primary productivity and decomposition rates will probably increase for a number of years.

Birds

Hemlock defoliation from HWA, even without hemlock mortality, represents the loss of important habitat, and is expected to significantly impact populations of several bird species. Because HWA-induced hemlock defoliation typically progresses from the lower to the upper crown, species dependent on the lower and middle hemlock crown will be affected first. Solitary vireos forage and nest in the lower levels of hemlock crowns, and black-throated green warblers forage and nest in the middle levels (Benzinger 1994b). Populations of both these species will probably be severely impacted in HWA-infested areas. Blackburnian warblers may be less immediately and directly impacted by HWA defoliation, because they nest in the highest levels of the hemlock canopy. However, their foraging and breeding success may be adversely affected by habitat changes lower in the canopy, and hemlock mortality is expected to severely impact local blackburnian populations. Extensive hemlock mortality, creating forest gaps, could provide invasion opportunities for avian nest predators and parasites, such as blue jays (*Cyanocitta cristata*) and cowbirds (*Molothrus alter*) (Lapin 1994). Populations of woodpeckers, cavity nesters, and bird species associated with hardwoods and earlier successional stages can be expected to increase in affected areas.

Streams

Defoliation by HWA will probably result in pronounced changes in energy and nutrient inputs (solar radiation, leaf litter) to streams with substantial riparian hemlock. Defoliation will allow more solar radiation (light) into a stream, and probably result in higher summer stream temperatures. Since all biological processes (e.g. growth and development) are temperature sensitive (especially in aquatic environments), higher summer temperatures will have myriad effects. Increased light and temperature, especially in combination with possibly elevated nutrient (nitrogen, phosphorus) levels, will increase stream primary productivity, and probably result in algal (periphyton) "blooms." Gypsy moth (*Lymantria dispar*) defoliation of the riparian tree canopy of a Rhode Island stream increased solar radiation penetration from less than 18% to over 70% of

incident values, and increased stream temperature 3.7°C (Sheath et al. 1986). In response, algal productivity increased, and the proportion of stream bottom covered by algae increased from below 35% to 80% (Sheath et al. 1986). Gypsy moth frass probably also increased nitrogen inputs and concentrations in this stream, but these were not measured. Defoliation by the fall cankerworm (*Alsophila pometaria*) accompanied substantial increases in stream concentrations and export of nitrate nitrogen from three mixed hardwood watersheds in North Carolina (Swank et al. 1981).

Increased primary production and inputs of deciduous leaf litter would lead to increased detritus processing and secondary production (aquatic invertebrates and fish). Sites with steep slopes (e.g. ravines) could experience increased erosion, sedimentation, and runoff rates, and changes in physical habitat characteristics such as stream channel shape and substrate composition. Eventually, the number of fallen hemlock logs (which are very resistant to decomposition) in and around affected streams would increase. Changes in fish species composition are likely. Brook trout populations may be eliminated because of increased temperatures, light intensity, habitat changes, and competition with other species. In many areas, native brook trout must compete with introduced (European) brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*), and higher temperatures provide a competitive advantage to these introduced species (Flebbe 1994).

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