

Chapter 4. Influence of eastern hemlock (*Tsuga canadensis*) on stream habitat in Delaware Water Gap National Recreation Area and its relationship to biological diversity patterns.

Craig D. Snyder, David P. Lemarie, John A. Young, David R. Smith,
Robert M. Ross and Randy M. Bennett

INTRODUCTION

Biological organization of stream communities is determined in large part by local habitat structure (Southwood 1977). Most aquatic invertebrates and fish species have evolved behavioral and/or morphological adaptations to specific habitat conditions including thermal regimes (e.g., Brandt et al. 1980, Sweeney 1984), substrate sizes (e.g., Minshall 1984, Ross et al. 1987), and flows patterns (Newbury 1984, Coon 1987). Consequently, their occurrence and abundance is highly dependent on availability of preferred habitat conditions. Furthermore, because resources required by aquatic species often vary with season and life cycle stage, the variety and distribution of available habitat types within a stream reach may limit aquatic diversity (Bayley and Li 1996). Finally, the physical conditions within a habitat, and the frequency and magnitude of disturbance events mediate levels of available food resources, and thus constrain competition and predation (Peckarsky and Dodson 1980), thereby indirectly influencing aquatic community structure.

Likewise, local habitat conditions are determined by patterns and processes in the surrounding watershed (Frissel et al. 1986, Poff 1997). Topography, geology, and soils are all important regulators of instream habitat. Of particular importance is the amount and composition of upland and riparian vegetation (see Chapter 2, Introduction section). Consequently, alterations to terrestrial components of the watershed can be expected to have significant consequences to the abundance and distribution of species, and ultimately to the diversity of aquatic assemblages, through their effects on local habitat.

We reported earlier that aquatic invertebrate diversity and brook trout occurrence were significantly higher in streams draining hemlock forests than those draining hardwood forests (Chapters 2 and 3). The purpose of this chapter is to compare local habitat conditions in streams draining hemlock and hardwood forests in an effort to determine the specific mechanism by which hemlock influences biological structure in Delaware Water Gap National Recreation Area.

METHODS

Habitat Sampling

Instream habitat measurements included those for water and the stream channel and were taken within the same stream reaches used to collect fish and macroinvertebrates (Chapters 2 and 3). Water chemistry measurements were taken at each site during spring high-flow conditions (proximate to invertebrate sampling) and summer base-flow conditions (proximate to fish sampling), except temperature which was collected once per hour for an entire year. We were unable to get summer water chemistry measurements for over half of our study sites because they dried up. As a result, we only report spring data. Water chemistry measurements were taken from well-mixed areas within the sample reaches. Water chemistry parameters measured and the instruments used are summarized in Table 4-1.

Table 4-1. Water temperature, water chemistry and hydrology parameters measured in DEWA streams. Type of instruments used and their associated accuracies are also reported.

Parameter	Accuracy	Instrument
Temperature (EC)	±0.02	Onset StowAway temperature logger
Dissolved oxygen (mg/L)	±0.01	Hydrolab Reporter Multi-probe water chemistry meter or Yellow Springs Instruments (YSI) Model 58 Dissolved Oxygen Meter
pH (-log H ⁺ ions)	±0.01	Hydrolab Reporter Multi-probe water chemistry meter
Specific conductance (ms/cm)	±1	Hydrolab Reporter Multi-probe water Chemistry meter or YSI Model 33 S-C-T meter
Turbidity (NTU)	±0.01	LaMotte turbidity meter (Model 2008)
Nutrients (mg/L)		Hatch DR/2000 Direct Reading Spectrophotometer
Total nitrates	±0.01	
Total nitrites	±0.001	
Reactive phosphates	±0.01	
Ammonia	±0.01	
Water Velocity (ft/sec)	±0.01	Marsh-McBirney FloMate model 2000 or model 201D portable flow meters

Temperature was measured hourly between 01 April 1997 and 31 March 1998 at 10 sites (i.e., two replicate site pairs for each of the five different stream types; Fig. 1-6) using Onset temperature loggers (Table 4-1). Two loggers were placed in each stream; one near the bottom of each of the sample reaches where fish and invertebrates were collected, and one between 300 and 1200 meters upstream depending on stream size. Loggers at two sites were lost and so analyses were confined to the remaining eight site pairs.

Stream channel measurements were taken during the period of base flow (July 1997) and included estimates of canopy cover, amount of large woody debris (LWD), and the extent to which streams dried up. Canopy cover (% of stream covered by overhanging vegetation) was measured with a Model A Spherical Densiometer (Forest Densiometers, Bartlesville, OK) at three points within each stream reach (top, middle, and bottom). We counted the number of pieces of large woody debris (LWD) of each of seven size classes (Table 4-2) throughout the entire sample reach. The extent to which streams dried during up during the summer was estimated visually to the nearest 10%. Each stream was subsequently classified into one of four categories based on the amount of 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. Finally, the microhabitat type (Table 2-1, Chapter 2) was recorded at the location where each invertebrate sample was taken. This allowed us to calculate patch richness (i.e., number of different microhabitat types) for each site.

Table 4-2. Classification of large woody debris size classes used to census DEWA streams. Taken from Dolloff et al. (1993).

Class	Diameter (cm)	Length (m)
1	5-10	1-5
2	10-50	1-5
3	>50	1-5
4	5-10	>5
6	>50	>5
7	Root Wad	

Analysis

We compared the differences in most local habitat characteristics between forest types using essentially the same methods as those used to compare invertebrate community structure (Chapter 2). That is, we used general linear modeling to test whether mean differences among site pairs for each response was equal to zero. We compared temperature data to make inferences regarding differences in thermal stability among forest types. Specifically, differences in temperature patterns (means, maxima, minima, and diurnal variation) among site pairs were summarized from hourly temperature data at each site and compared graphically. Finally, We used Fisher's Exact Test to test the hypothesis that streams that dried up were were equally represented between hemlock and hardwood forests. We used StatExact (Mehta and Patel 1997) to calculate Fisher's test statistics and exact p-values.

RESULTS

Water Chemistry and Physical Habitat

Forest type did not have a significant effect on any of the eight water chemistry variables for any single stream type (Fig. 4-1). Since mean differences in water chemistry between forest types were not different among stream types (ANOVA, $p > 0.27$ for all eight variables), we pooled differences across stream types. Overall, dissolved oxygen was higher, and specific conductance, turbidity, and total nitrites were lower in streams draining hemlock forests than those draining hardwood (Fig. 4-1, pooled).

With respect to the stream channel, we found microhabitat patch richness (i.e., numbers of different microhabitat types) was higher in streams draining hemlock for most stream types (Fig. 4-2). However, like invertebrate species richness and Shannon diversity index described earlier (see Chapter 2), the pattern shown by 1st order, mid-slope sites deviated substantially from those of the other stream types. Mean differences in microhabitat richness were not different among stream types when 1st order midslope sites were excluded (ANOVA, $F = 1.029$, $p = 0.436$). However, microhabitat differences were significantly different between forest types when midslope sites were included ($F = 3.007$, $p = 0.078$). Results from data pooled across all stream types except 1st order mid-slope sites suggest a significant forest type effect on stream microhabitat diversity except in 1st order, mid-slope sites. However, higher microhabitat patch richness observed in streams draining hemlock was not associated with any particular microhabitat types. That is, of the 30 microhabitat types represented in DEWA streams (Table 2-1), none were found to be significantly more common in streams draining hemlock (Results of 2X2 Fishers Exact Tests > 0.2 for all habitat types).

In contrast, we found no overall differences in large woody debris (LWD) or percent canopy cover in streams draining hemlock and mixed hardwood forest types. We observed no significant differences in LWD density (i.e., number of pieces per 100 m stream length) of any of the seven size classes between forest type, or between terrain type and stream order (Multi-response Permutation Procedures, $p > 0.25$ for all three design variables). Likewise, canopy cover was not significantly different between streams draining hemlock and hardwood forest types. However, these measurements were only taken during mid-summer leaf-on. Clearly the deciduous watersheds would contribute substantially less canopy cover during winter leaf-off, and it is very likely that percent cover would be greater in streams draining hemlock if measurements were integrated over the entire year.

Thermal Patterns

We observed a significant forest type effect on thermal patterns at several of our sampling sites. Specifically, median daily temperature tended to be cooler in the summer, warmer in the winter, and less variable throughout the year at study sites draining hemlock forests (Fig. 4-3). However, the pattern described above was not consistent, occurring at only four of eight site pairs where temperature patterns were measured. As with biological differences, the two mid-slope site pairs showed essentially the opposite pattern, and no differences were observed between forest types for two other site pairs (Fig. 4-3).

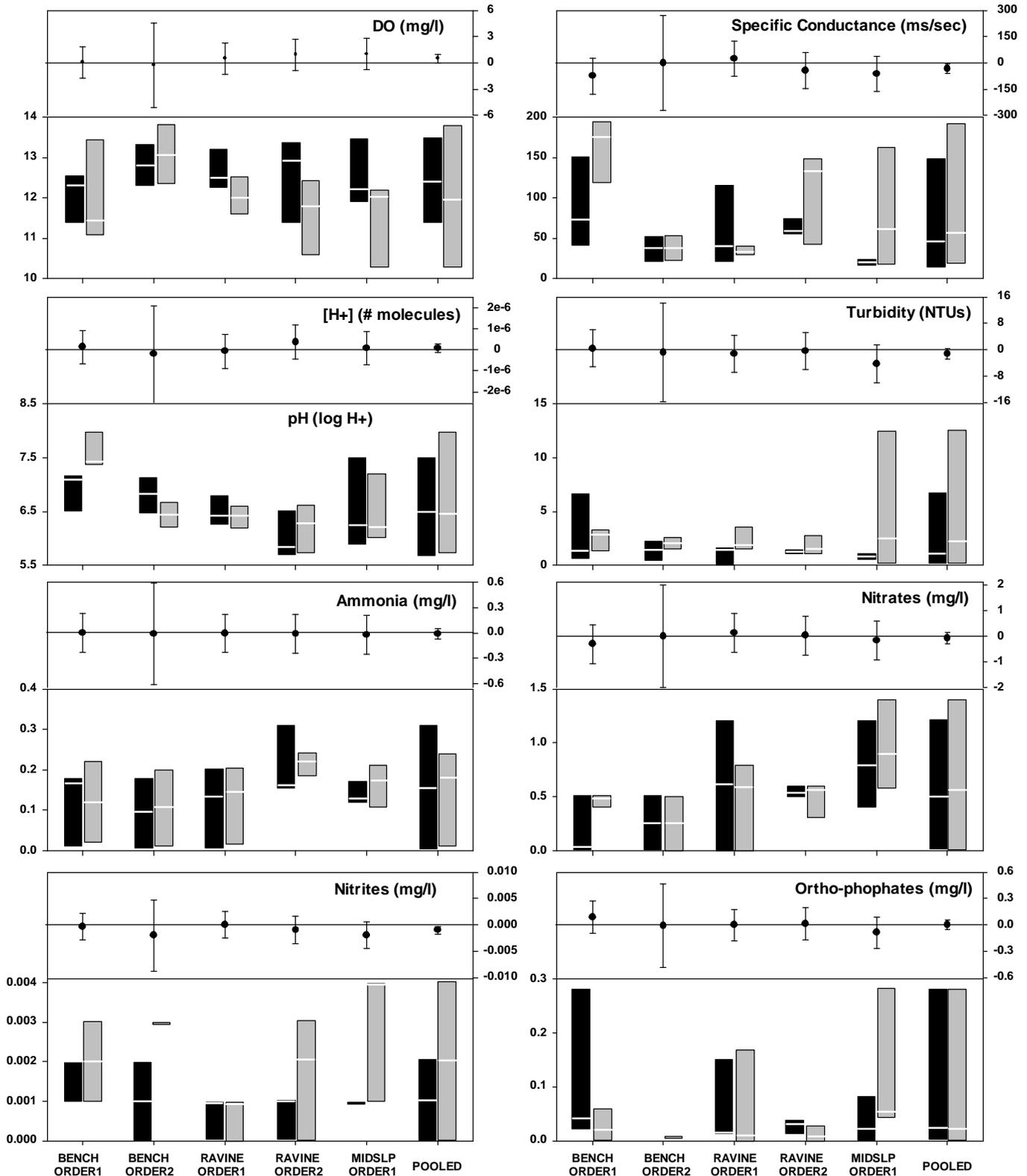


Figure 4-1. Comparison of eight water chemistry variables between streams draining hemlock and hardwood forest types. Top panel shows mean differences (+/- 90% C.L.) between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Bottom panel compares the range of values (limits of box) and medians (white lines) between forest types (hemlock=black bars). Comparisons are made within each stream type as well as pooled across stream types (ALL).

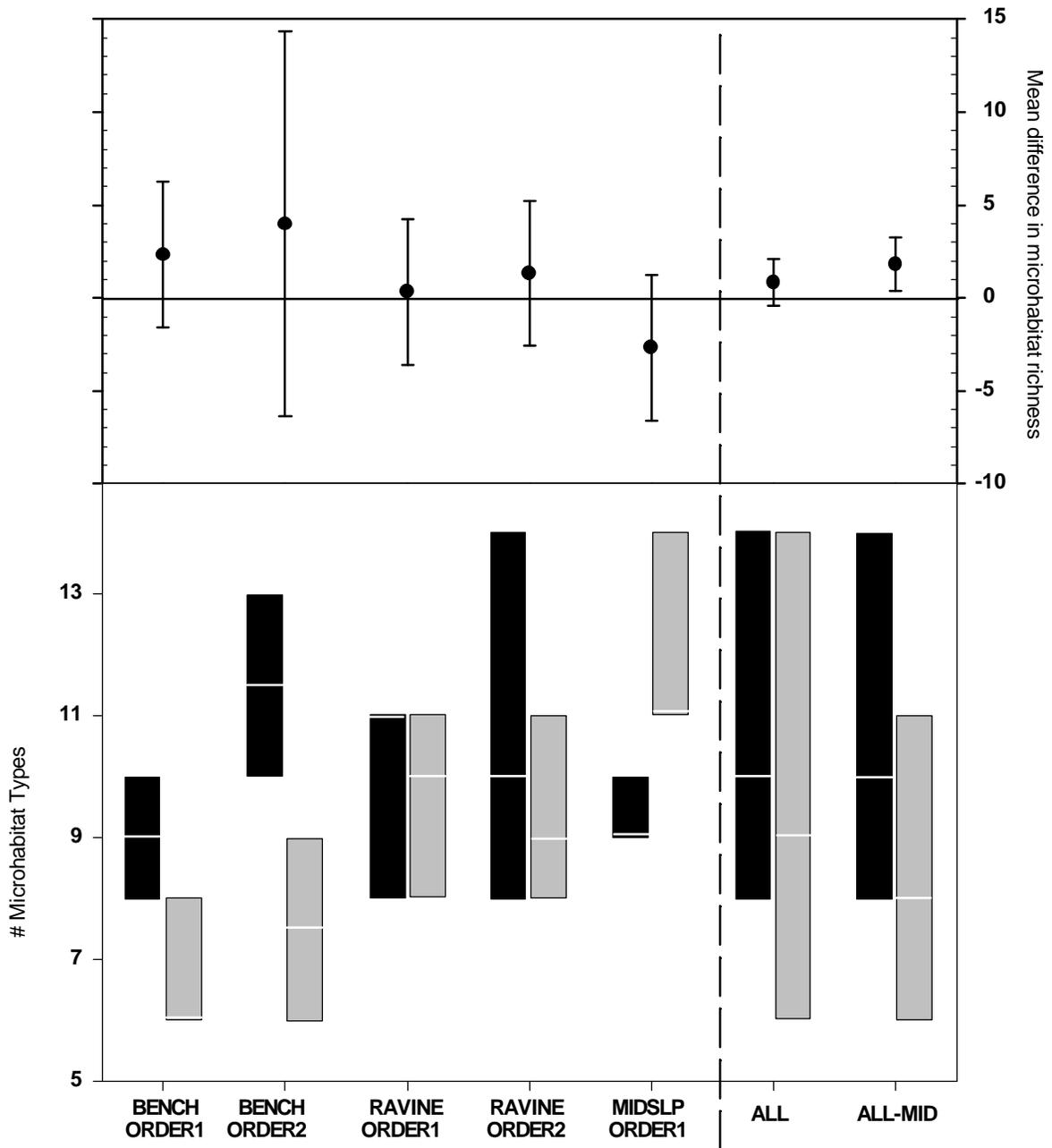


Figure 4-2. Comparison of microhabitat patch richness between streams draining hemlock and hardwood forests. Top panel shows mean differences (\pm 90% C.L.) between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Bottom panel compares the range of values (limits of box) and medians (white line) between forest types (hemlock=black bars). Comparisons are made within each stream type as well as pooled across stream types (ALL) and all but midslope sites (ALL-MID).

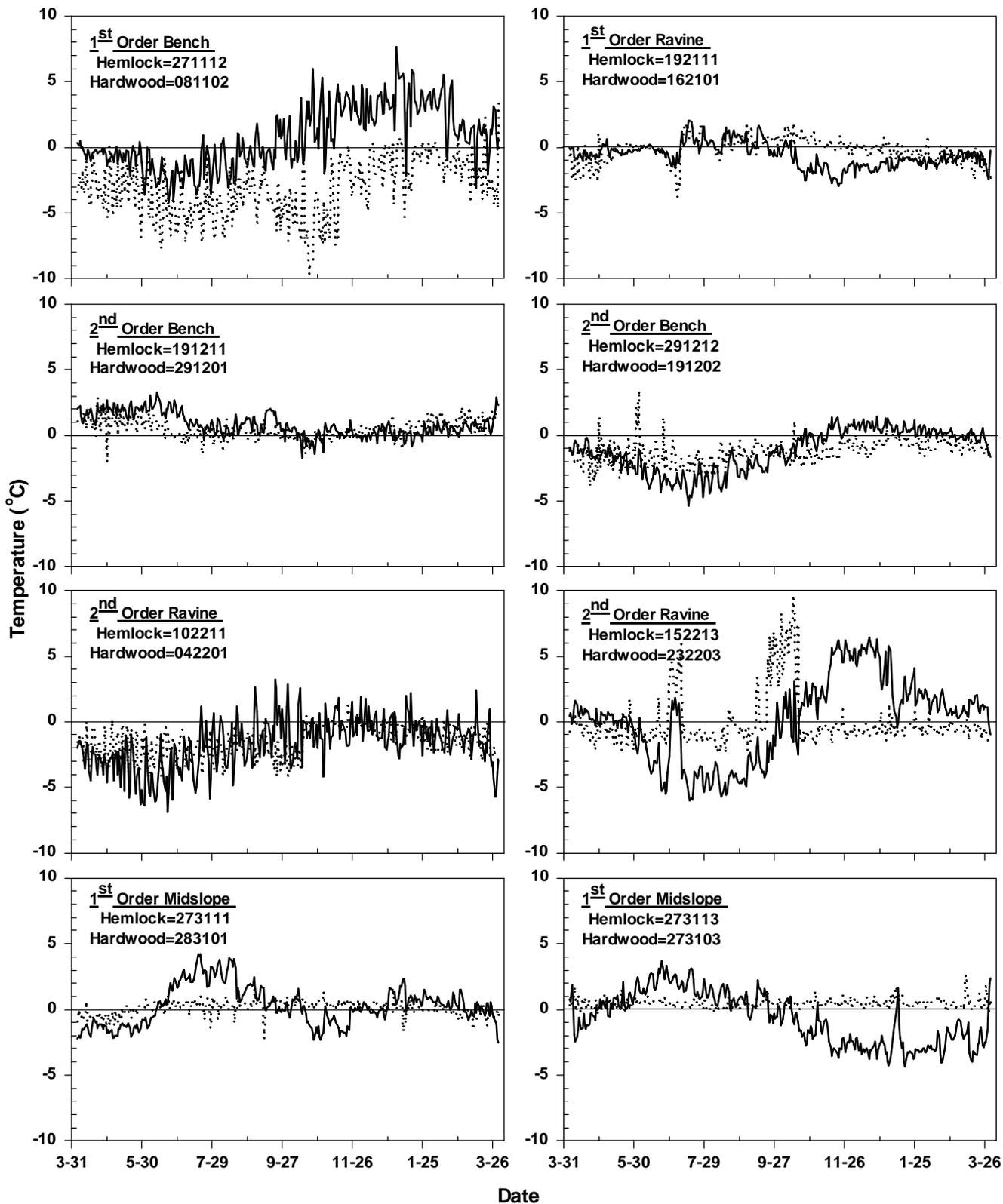


Figure 4-3. Differences in median daily temperature (solid line) and diurnal range (dashed line) between hemlock and hardwood site pairs between spring 1997 and spring 1998. Data from hardwood sites were subtracted from data from hemlock sites so values greater than 0 indicate hemlock was warmer (in the case of median line) or temperature was more variable (in the case of diurnal variation line). Stream type and site numbers are also shown.

The predominant pattern described above could have been produced in two ways. First, stream temperatures could have been different initially. That is, hemlock and hardwood forests may have had similar influences on stream temperatures but temperature patterns were different upstream, near stream sources. Second, surrounding vegetation could have influenced temperatures as water proceeded through the forest. We placed additional loggers several hundred meters upstream of study sites (Fig. 1-6) in an effort to determine changes in stream temperature patterns as water passed through the forest. Upstream-downstream differences in stream temperature suggested that indeed hemlock and hardwood forests differed in their respective influence on stream temperature. For example, during the summer, water passing through hemlock forests either cooled more or warmed less than water passing through their paired hardwood forests (Fig. 4-4). Likewise, during the winter, water tended to warm or remain relatively stable in streams draining hemlock while cooling substantially in paired hardwood forests (Fig. 4-4). In general, these patterns were consistent with the same four site-pairs described above. Again, both 1st order midslope sites showed the opposite pattern.

In addition, during the summer, streams draining hemlock tended to warm more slowly in response to warming air temperature than their hardwood counterparts (Fig. 4-5). Again, the pattern was consistent for three of the four site-pairs described above. Midslope sites again responded differently than the other stream types and no differences due to forest type were observed for the 1st order ravine site pair and one of the 2nd order bench sites (Fig. 4-5). Also, one of the two 2nd order ravine site pairs showed a different pattern where there was essentially no relationship at all between air and water temperature for much of the summer. However, we believe that this is due in large measure to ground water influence on the temperature of the stream draining the hardwood forest. Temperatures remained almost constant during much of the summer at that site. Those occasions when temperature did fluctuate (dotted line figure 4-5) suggested that water temperature responded in the same way as the other three site pairs (i.e., more dramatically in the hardwood than hemlock site) when surface water flow predominated.

Probably more important than mean, medians and other measures of central tendency to fish and invertebrates are the seasonal extremes in temperature. With the exception of mid-slope sites, summer maxima were higher in streams draining hardwood forests (Fig. 4-6). For example, summer maxima in streams draining hardwood forests exceeded 20°C over 18% of the time compared to less than 3% in streams draining hemlock. Likewise, winter minima were lower in streams draining hardwood (Fig. 4-6). Minimum temperatures dropped below freezing 8% of the time in hardwood sites compared to only 0.2% in hemlock sites. Taken together, differences in temperature patterns between forest types suggest that streams draining hemlock were less extreme and more stable.

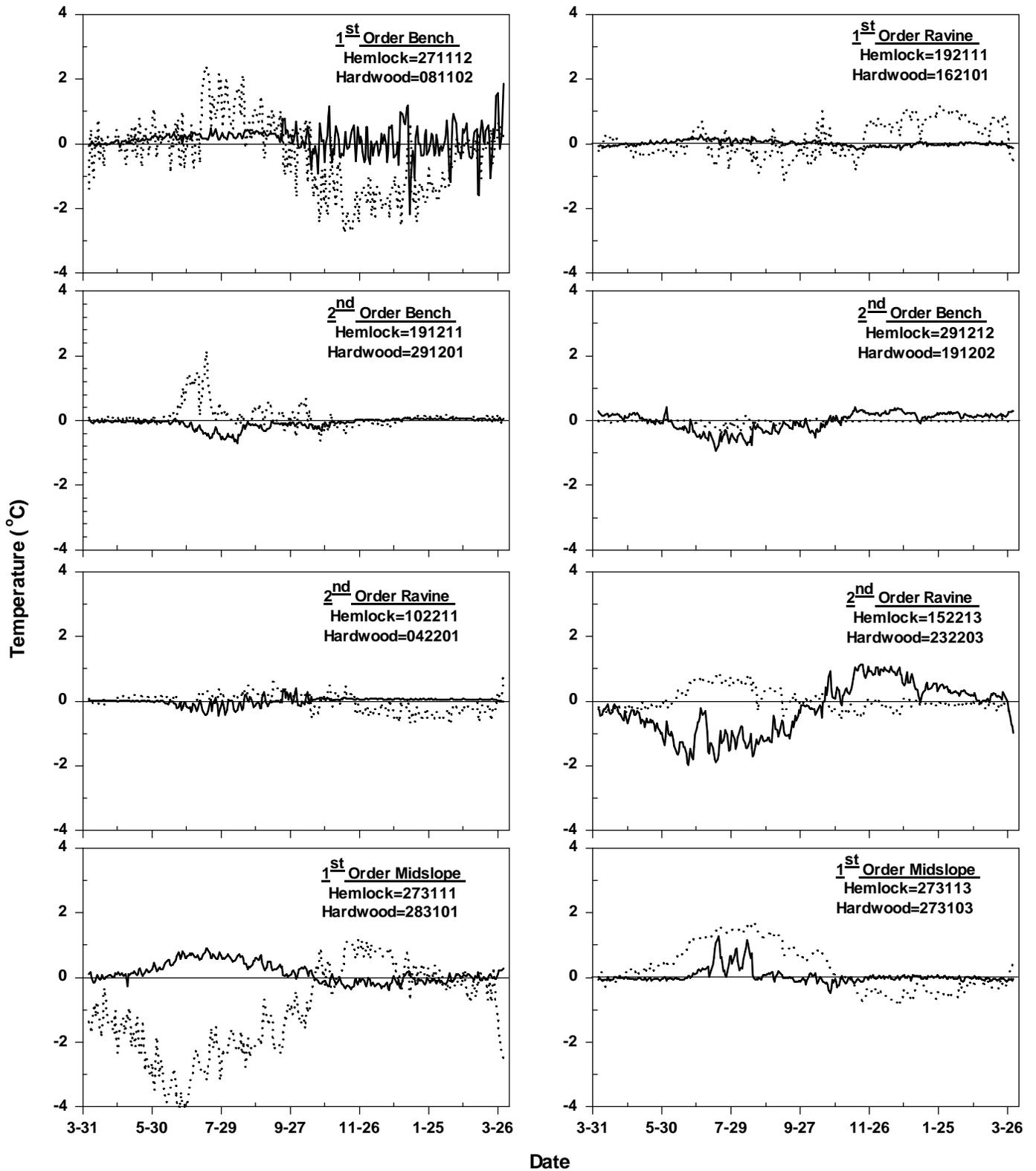


Figure 4-4. Comparisons of the effects of forest type on average stream temperature. Changes in stream temperature per 100 meters of stream was calculated as the difference in mean daily temperature between a site at the bottom of the study reach and one several hundred meters upstream. Thus, positive values indicate stream temperature warmed as water progressed downstream. Solid lines refer to stream draining hemlock and dashed lines refer to the hardwood pair. Stream type and site numbers are shown.

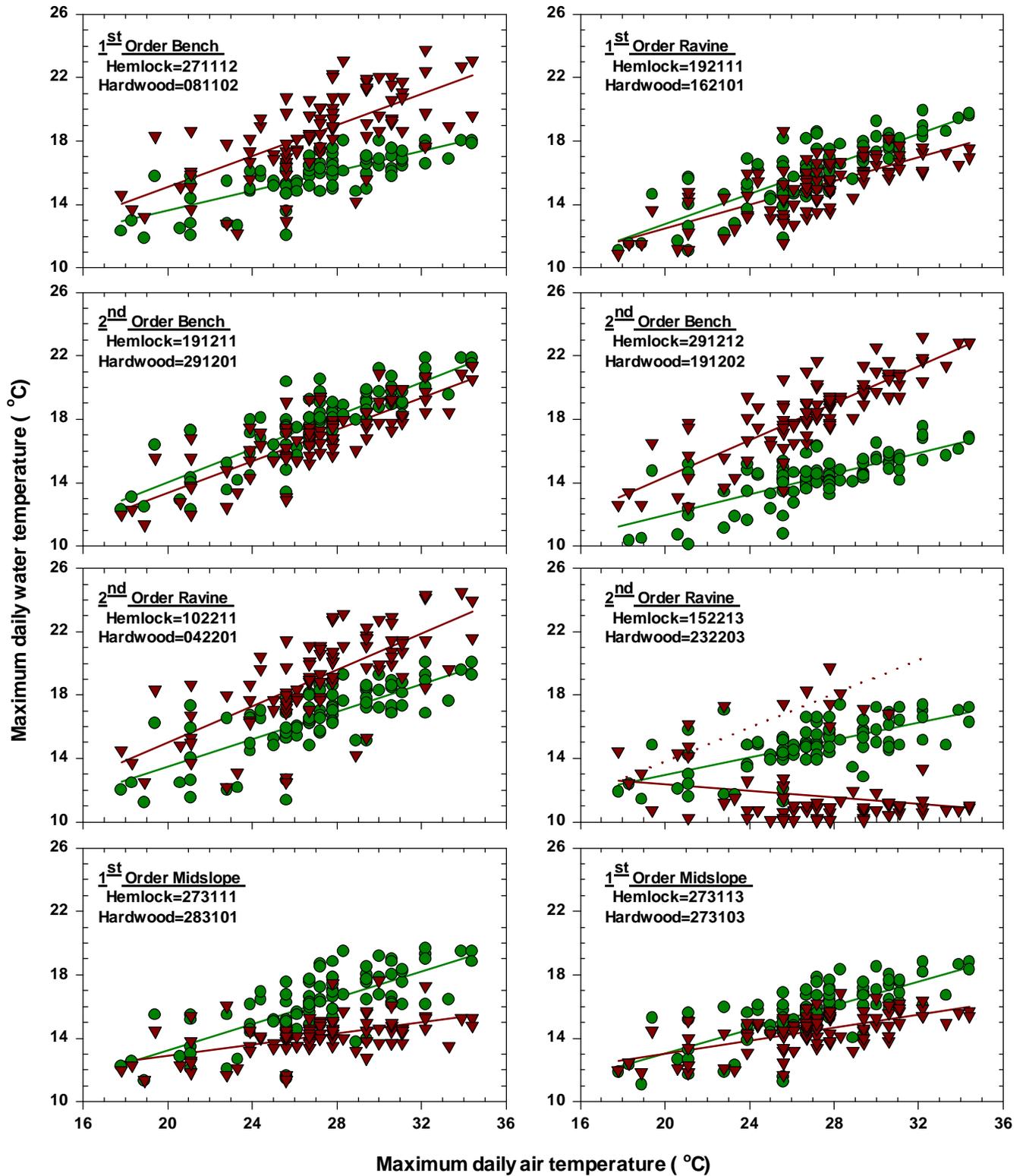


Figure 4-5. Comparison of air temperature - water temperature relationships between hemlock-hardwood site pairs. Data included observations between May and October 1997. Hemlock sites with green lines and symbols, hardwood sites with red.

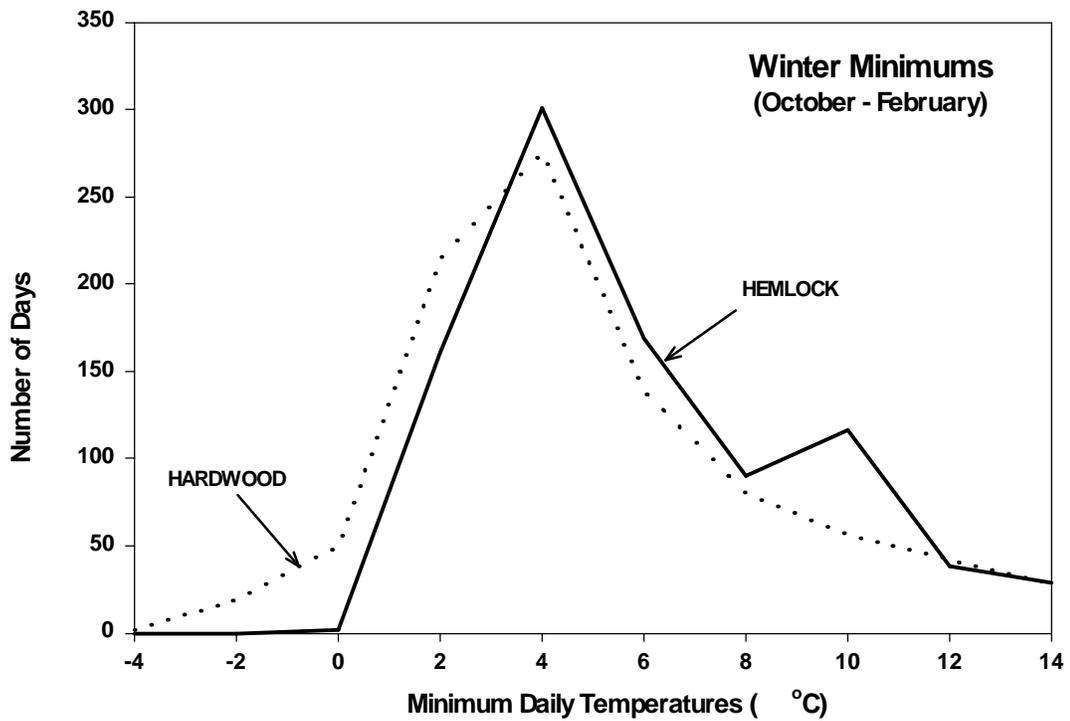
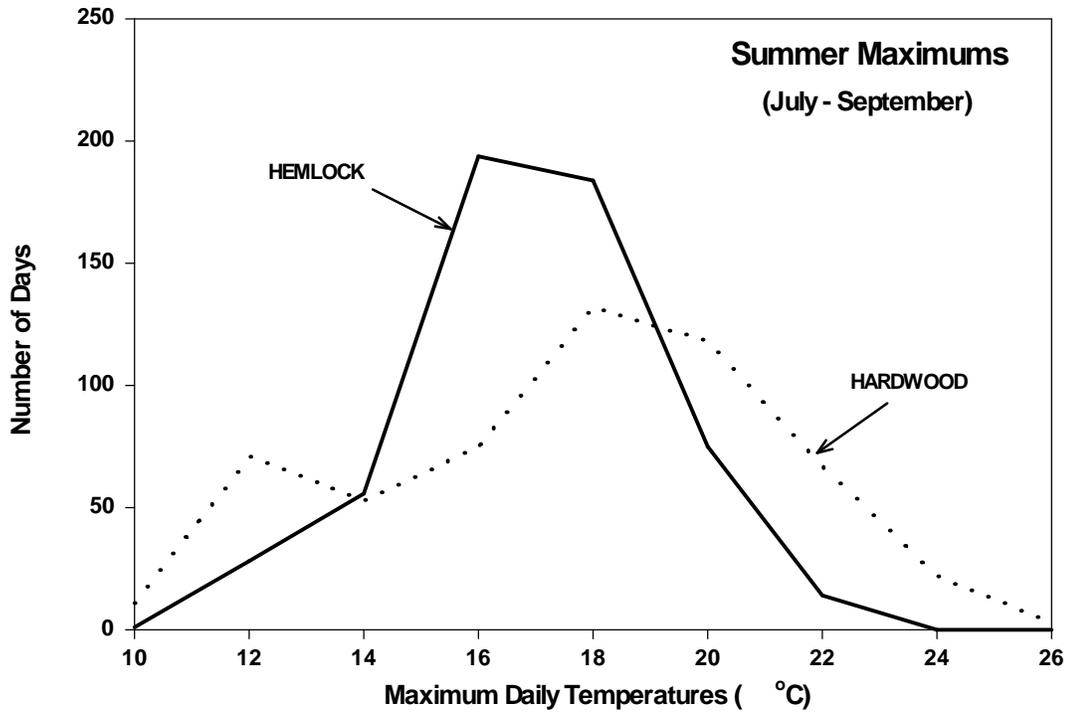


Figure 4-6. Comparison of the distributions of summer maximum temperatures (July-September) and winter minimum temperatures between streams draining hemlock and hardwood forests. Data from first order mid-slope sites were omitted because both temperature patterns and diversity patterns differed from those of the other stream types.

Hydrologic Patterns

We used flow data from the USGS gaging station on the Bushkill River to characterize rainfall patterns throughout the Park. We found stream flows to be normal (i.e., close to the long-term average) during the spring, when invertebrate sampling was conducted. However, the summer 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 (Fig. 4-7).

The result of the dry summer in 1997 was that a substantial portion of our study streams dried up. However, streams draining hardwood forests dried significantly more than their hemlock pairs (Table 4-3; $\chi^2=9.429$, $df=3$, $p=0.024$). These patterns suggest that in particularly dry years, streams draining hardwood forests are more likely to dry, and fish and invertebrates would be unable to complete their life cycles.

Table 4-3. Extent to which DEWA study streams dried up during the summer of 1997. Extent of drying was estimated visually to the nearest 10% of the stream channel bottom between 07 July and 16 July, 1997 when fish collecting occurred. Mostly wet = >50% of stream bottom was wetted; mostly dry = <50% of stream bottom wetted. See Table 1 in Chapter 3 for more detail.

	Number of Sites (%)	
	Hemlock (N=14)	Hardwood (N=14)
Completely Dry	0 (0.0%)	4 (28.6%)
Mostly Dry	2 (14.3%)	5 (35.7%)
Mostly Wet	3 (21.4%)	0 (0.0%)
Wet	9 (64.3%)	5 (35.7%)

DISCUSSION

There are several mechanisms by which the composition of streamside vegetation can influence fish and aquatic invertebrate communities. The most direct influence would be in regulating the amount and quality of energy inputs. Headwater streams in relatively undisturbed, forested catchments are largely heterotrophic because surrounding vegetation both limits primary production through shading, and directly provides energy in the form of leaves and wood that fall into the stream (Cummins 1992). Thus, forest-specific differences in the quantity, timing, and variety of leaf litter inputs could affect the distribution and abundance of aquatic species. There is some evidence that hemlock and other conifers contribute more allochthonous inputs annually than mixed hardwood forests (Anderson and Sedell 1979, Molles 1982). On the other hand, there is also evidence that shredder invertebrates prefer hardwood leaf species and do not grow as well when fed conifer or deciduous evergreen needles (Anderson and Grafius 1975). Thus, it is unclear what the net effect of forest-specific differences in allochthonous inputs would be on aquatic biodiversity.

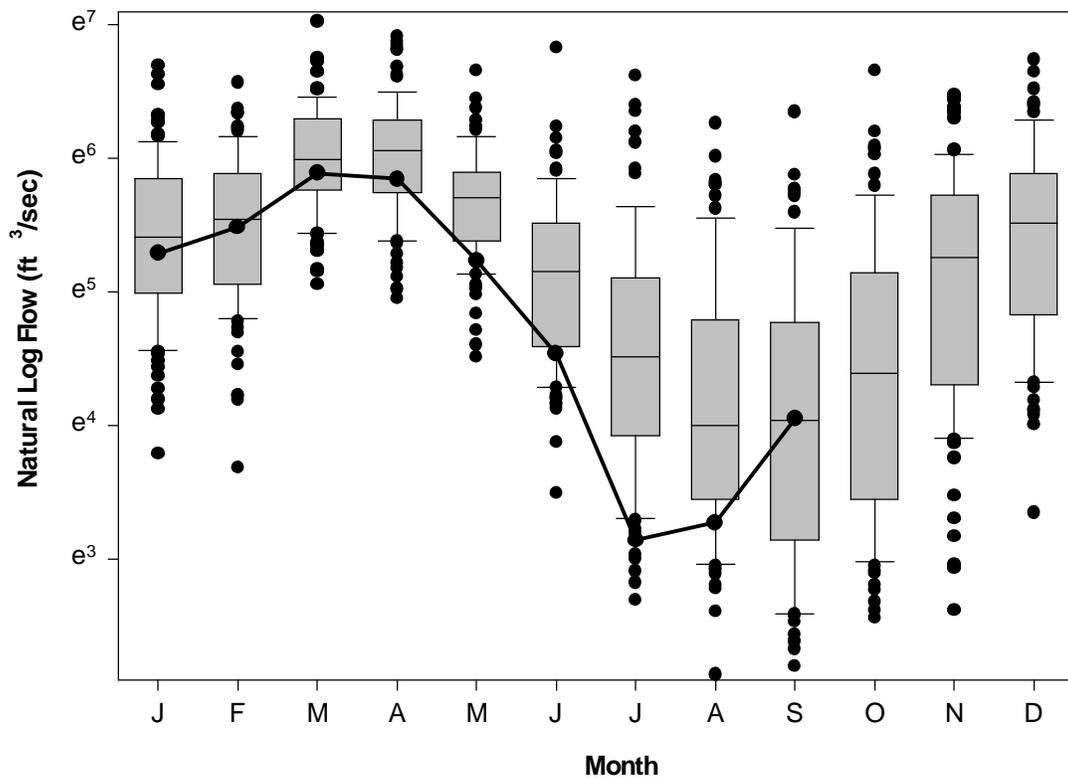


Figure 4-7 . Box plots show the distribution of mean flows at the Bushkill River gaging station (#01439500) at Shoemakers, PA, for a 90 year period between 1908 and 1997. Solid lines within each box plot represents the median, the limits of the box represent 50% of the values, limits of error bars represent 90% of the values, and individual points represent the remaining data. The solid line shows median discharge for the 1997 study year. Data taken from USGS web site (<http://waterdata.usgs.gov/nwis>)

We did not measure leaf litter inputs directly. However, there is some indirect evidence that leads us to believe that differences in energy subsidies between forest types were not responsible for higher aquatic invertebrate diversity and brook trout occurrence observed in streams draining hemlock forests. First, if diversity differences were due to the presence of hemlock needles as an additional or alternative food source, we would expect the shredder-detritivore trophic group to be most affected. Shredding insects are the first macroinvertebrates to use leaf litter as food and tend to be the most selective of all the detritus feeders (Anderson and Sedell 1979). However, we found no significant differences in shredder diversity between forest types (Fig. 2-2). Secondly, if the quantity of leaf litter was higher in streams draining hemlock, we would expect higher total densities in addition to higher diversity. This was also not the case as total densities were actually significantly higher in streams draining hardwood (Fig. 2-1).

Another mechanism by which streamside vegetation can influence aquatic community structure is the role that large woody debris plays in controlling the amount and distribution of microhabitats. In addition to directly adding habitat complexity by providing additional substrate for invertebrates and cover for fish (O'Conner 1991, Richards and Host 1994), presence of large woody debris in streams creates barriers to flow and consequently facilitates the formation of dam and scour pools, thereby increasing microhabitat diversity (Swanson and Lienkaemper 1978, Gregory 1992). In addition, large woody debris increases retention time of organic matter and nutrients required by aquatic species (Bilby 1981, Harmon et al. 1986). Moreover, there is evidence that hemlock forests contribute substantially more woody debris to streams they drain than corresponding mixed hardwood forests (Anderson and Sedell 1979), and that conifer wood decays much more slowly than hardwoods (Harmon et al., 1986). Therefore, streams draining hemlock may be expected to have a more complex habitat structure that could directly and/or indirectly influence both fish and invertebrate diversity and abundance.

In DEWA, streams draining hemlock had significantly higher microhabitat diversity overall than their hardwood counterparts, and this pattern was consistent for most stream types (Fig. 4-2). However, we observed no differences in the amount and size distribution of LWD between streams draining hemlock and mixed hardwood forests. Thus, other factors besides differences in large woody debris inputs between forest types could have been responsible for higher stream habitat diversity in hemlock-dominated watersheds. Although we tried to account for variation in terrain in our study design, it could be that relatively subtle differences in topography could have profound differences on the distribution and abundance of microhabitats. However, residence time for woody debris in streams is highly variable (Gregory 1992) and the influence of large woody debris on the processes that control channel morphology and microhabitat diversity are long-term. Thus, it could also be that higher microhabitat diversity observed at hemlock sites was created by higher large woody debris inputs in years past or the cumulative inputs over a long period of time. Although the relationship between microhabitat diversity and aquatic macroinvertebrate diversity was not entirely consistent (i.e., site pairs where the hemlock stream had significantly more microhabitat types were not always the same site pairs where invertebrate diversity was higher in the hemlock site and visa versa) these data suggest hemlock effects on microhabitat diversity could have been partially responsible for the observed community structure differences.

Upland and riparian vegetation also have a profound influence on instream nutrient dynamics (e.g., Pinay et al. 1990). For example, in a study comparing nutrient processing rates between hemlock and sugar maple (*Acer saccharum*) forests, Mladenoff (1987) found nitrogen mineralization rates (i.e., proportion of available nitrogen used) to be higher in hemlock suggesting hemlock forests are more efficient in removing nitrogen from soils. Consequently, nitrogen concentrations in streams draining hemlock forests may be expected to be lower than in streams draining hardwood forests. Furthermore, nitrogen processing rates have been shown to increase dramatically with hemlock woolly adelgid-induced hemlock mortality (Jenkins 1998).

In turn, nutrient loads can affect aquatic communities by increasing primary and secondary productivity (e.g., Hall et al. 1970) and by depleting oxygen levels (Wetzel 1983). Although no differences in phosphates, ammonia, and nitrates were observed between forest types, total nitrites were significantly lower in streams draining hemlock (Fig. 4-1). However, we believe it is unlikely that differences in nitrite levels had a significant effect on aquatic community structure at our study sites. Light is probably at least as important in limiting primary production as nutrients in these low-order streams, and oxygen levels are near saturation throughout the year due to the continuous mixing associated with turbulent flow patterns in high gradient watersheds.

Finally, streamside vegetation exerts considerable control on stream temperature and flow patterns. For example, in the extreme, forest removal increases stream temperatures (Swift and Messer 1971) and results in more extreme (i.e., higher highs and lower lows) flow patterns (Graf 1980). We were unable to find any published information that compared the relative effects of hemlock and other forest types on thermal and hydrologic patterns. Nevertheless, hemlock forests may be expected to provide more shading annually than mixed hardwood forests. This may provide a blanket effect, where cumulative temperature and moisture levels remain more stable.

Low order, high gradient streams such as those sampled in this study, are generally believed to be disturbance-controlled. That is, the diversity and structure of aquatic communities are influenced more by the frequency and magnitude of floods, droughts, and temperature extremes than by more deterministic factors such as predation and competition (Resh et al. 1988, Grossman et al., 1990). Thus, factors that enhance environmental stability would be expected to have positive effects on the diversity of aquatic communities. Empirical studies with invertebrates (e.g., Death and Winterbourn 1995) and fish (Grossman et al. 1982) support this general hypothesis.

We found some evidence that hemlock forests had a significant buffering effect on thermal patterns. In general, stream temperatures at hemlock sites were less sensitive to changes in air temperature (Fig. 4-5) resulting in cooler summer temperatures and warmer winter temperatures (Fig. 4-3). Furthermore, summer and winter extremes in temperature were more moderate in streams draining hemlock (Fig. 4-6). This buffering effect could 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 (Fig. 4-6) strongly supports the conclusion that a hemlock-induced effect on moderating stream temperatures was responsible for the distribution and occurrence patterns of brook trout that we found.

There was also evidence that the extent to which streams dried up was influenced by forest type. Fewer of the streams draining hemlock forests dried up (Table 4-3), possibly owing to the temperature differences described above. Although 1997 represented a particularly dry summer (Fig. 4-7), organisms at DEWA can expect to be subjected to conditions as dry or drier every 11 years (recurrence interval calculated from gaging station data in figure 4-7 using Weibull probability method as described in Gordon et al., 1992). Clearly, during such dry years, a large fraction of both fish and invertebrates will fail to survive and reproduce. Consequently, their occurrence and abundance at sites that frequently dry will be largely determined by re-colonization potentials. In contrast, streams that maintain sufficient flows during dry years will most certainly support more species.

In summary, no single habitat variable directly correlated with aquatic invertebrate diversity or brook trout occurrence differences observed between forest types (Chapters 2 and 3). However, we found forest type had a significant, concomitant influence on several habitat variables, each of which could have contributed to some extent, to the observed differences in aquatic community structure. Although hemlock effects on microhabitat diversity and nutrient concentrations may have contributed to aquatic community differences observed between forest types, we believe that hemlock mediated increases in thermal and hydrologic stability were most important in explaining higher invertebrate diversity and brook trout occurrence patterns.

From a broader perspective, the observed hemlock effects on stream conditions may have an influence in other parts of the drainage basin. For example, although higher nitrite concentrations in streams draining hardwood forests are likely to have a minimal effect on biological communities in these small, high gradient streams, the cumulative effect on the Delaware River and ultimately the Delaware Bay could be significant if hemlock forests throughout the basin die and become replaced by hardwood. Nutrient levels in the Delaware River are of particular concern and specific nutrient limits have been established (Delaware River Basin Commission Water Quality Regulations 1996). If hemlock forests within DEWA succumb to HWA and are replaced, as expected, by mixed hardwoods, then nitrite levels may be expected to increase in the Delaware River. Such increases could increase primary production and decrease dissolved oxygen levels in the River and the Bay. Likewise, hemlock-mediated increases in thermal and hydrologic stability may also cascade to other portions of the basin. Survival and productivity of Delaware river fishes, particularly trout and shad, may be limited by the relative severity of summer, base-flow conditions. Stable discharges of cooler water from hemlock-dominated watersheds may provide refugia during these summer extremes.

LITERATURE CITED

- Anderson, N.H. and E. Grafius. 1975. Utilization and processing of allochthonous material by stream Trichoptera. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 19:3022-3028.
- Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of the Entomological Society* 24:351-377.
- Bayley, P. B. and H. W. Li. 1996. Riverine fishes. Pages 92-122 in G. E. Petts and P. Calow (editors). *River Biota: Diversity and Dynamics*. Blackwell Science Publishers, Cambridge, MA.
- Bilby, R.E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology* 62:1234-1243.
- Brandt, S. B., J. J. Magnuson, and L. B. Crowder. 1980. Thermal habitat partitioning by fishes in Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1557-1564.
- Coon, T. G. 1987. Responses of benthic riffle fishes to variation in stream discharge and temperature. Pages 77-85 in W. J. Matthews and D. C. Heins (editors). *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman, OK.
- Cummins, K.W. 1992. Catchment characteristics and river ecosystems. Pages 125-135 in P.J. Boon, P. Calow, and G.E. Petts (editors). *River Conservation and management*. John Wiley and Sons, Inc., NY.
- Delaware River Basin Commission Water Quality Regulations: Administrative Manual Part III. 1996. Delaware River Basin Commission, West Trenton, NJ.
- Death, R.G. and M.J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: The influence of habitat stability. *Ecology* 76:1446-1460.
- Dolloff, C. A., D. G. Hankin, and G. H. Reeves. 1993. Basinwide estimation of habitat and fish populations in streams. General Technical Report SE-83. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experimental Station. 25pp.
- Frissel, C.A., W.J. Liss, C.E. Warren, and M.D. Hurley. 1986. A hierarchical framework for stream classifications: viewing streams in a watershed context. *Environmental management* 10:199-214.
- Gordon, N.D., T.A. McMahon, and R.L. Finlayson. 1992. *Stream Hydrology: An Introduction*

- for Ecologists. Wiley Publishers, West Sussex, England. Pages 526.
- Graf, W.L. 1980. Riparian management: a flood control perspective. *Journal of Soil and Water Conservation*. 35:158-161.
- Gregory, K.J. 1992. Vegetation and river channel process interactions. Pages 255-269 in P.J. Boon, P. Calow, and G.E. Petts (editors). *River Conservation and Management*. John Wiley and Sons Limited, West Sussex, England.
- Grossman, G.D., P.B. Moyle, and J.O. Whitaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: A test of community theory. *The American Naturalist* 120:423-454.
- Grossman, G.D., J.F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: A review. *Environmental Management* 14:661-671.
- Hall, D.J., W.E. Cooper, and E.E. Werner. 1970. An experimental approach to the production, dynamics, and structure of freshwater animal communities. *Limnology and Oceanography* 15:839-928.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaemper, K. Cromack, and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133-302.
- Jenkins, J. 1998. Measuring and modeling northeastern forest ecosystem response to environmental stresses. Ph.D. Dissertation, University of New Hampshire, Durham, New Hampshire 93824. Pages 147.
- Jenkins, R.E. and N.M. Burkhead. 1993. *Freshwater Fishes of Virginia*. American Fisheries Society, Bethesda, Maryland. Pages 1079.
- Mehta, C. and N. Patel. 1997. *LogXact for Windows*. User Manual. Cytel Software Corporation, Cambridge, MA, USA.
- Minshall, G. W. 1984. Aquatic insect-substratum relationships. Pages 358-400 in V. H. Resh and D. M. Rosenberg (editors). *The Ecology of Aquatic Insects*. Praeger Publishers, NY.
- Mladenoff, D.J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* 68:1171-1180.
- Molles, M.C. 1982. Trichopteran communities of streams associated with aspen and conifer forests: Long-term structural change. *Ecology* 63:1-6.
- Newbury, R. W. 1984. Hydrologic determinants of aquatic insect habitats. Pages 323-357 in V.

- H. Resh and D. M. Rosenberg (editors). *The Ecology of Aquatic Insects*. Praeger Publishers, NY.
- O'Conner, N.A. 1991. The effects of habitat complexity on the macroinvertebrates colonizing wood substrates in a lowland stream. *Oecologia* 85:504-512.
- Peckarsky, B. L., and S. I. Dodson. 1980. An experimental analysis of biological factors contributing to stream community structure. *Ecology* 61:1283-1290.
- Pinay, G., H. Decamps, E. Cauvet, and Elaine Fustec. 1990. Functions of ecotones in fluvial systems. Pages 141-169 in R.J. Naiman and H. Decamps (editors). *The Ecology and Management of Aquatic-terrestrial Ecotones*. The Parthenon Publishing Group Limited, NJ.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* 16:391-409.
- Resh, V.H., A.V. Brown, A.P. Covich, M.E. Gurtz, H.W. Li, G.W. Minshall, S.R. Reice, A.L. Sheldon, J.B. Wallace, and R. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433-455.
- Richards, C. and G. Host. 1994. Examining land use influences on stream habitats and macroinvertebrates: A GIS approach. *Water Resources Bulletin* 30:729-738.
- Ross, S. T., J. A. Baker, and K. E. Clark. 1987. Microhabitat partitioning of southeastern stream fishes: Temporal and spatial predictability. Pages 42-51 in W. J. Matthews and D. C. Heins (editors). *Community and Evolutionary Ecology of North American Stream Fishes*. University of Oklahoma Press, Norman, OK.
- Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:337-367.
- Swanson, F.J. and G.W. Lienkaemper. 1978. Physical consequences of large organic debris in Pacific North West Streams. USDA Forest Service, General Technical Report PNW-69, 1-13.
- Sweeney, B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56-100 in V. H. Resh and D. M. Rosenberg (editors). *The Ecology of Aquatic Insects*. Praeger Publishers, New York.
- Swift, L.W. Jr, and J.B. Messer. 1971. Forest cuttings raise temperatures of small streams in the southern Appalachians. *Journal of Soil and Water Conservation* 26:111-116.
- Wetzel, R.G. 1983. *Limnology* (second edition). Saunders College Publishing, Philadelphia, PA. 767 pages.