Chapter 2: Influence of eastern hemlock (*Tsuga canadensis*) on stream invertebrate community structure in small headwater streams of the Delaware Water Gap National Recreation Area.

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INTRODUCTION

It has become increasingly clear that the physical and biological structure of streams are inextricably linked to the status and condition of the surrounding watershed. For example, terrestrial leaf litter constitutes the main energy supply for forested headwater streams (Hynes 1975), and riparian vegetation acts synergistically with topography to influence instream habitat conditions (Bisson et al. 1987) and organic carbon and nutrient processing rates (Pinay et al. 1990). In turn, aquatic macroinvertebrates are primary consumers of terrestrial leaf litter and their distribution and production have been shown to correlate with components of the surrounding forests (Ross 1963). In addition, aquatic invertebrates represent a significant food source for fish and their feeding activity modifies the form and rate with which leaf material is processed and exported (Cuffney et al. 1990). Therefore, changes in macroinvertebrate community structure associated with forest disturbances may cascade to other aquatic assemblages. Furthermore, since emerging insects represent a significant energy source for birds, spiders and other terrestrial fauna (Jackson and Fisher 1986), macroinvertebrate responses may feed back to the terrestrial system as well. Thus, forest disturbance may have profound effects to the aquatic macroinvertebrate community and to the overall watershed ecosystem. However, most research has emphasized the short-term effects of forest removal on stream communities. There have been relatively few studies specifically designed to examine the long-term consequences of changing forest composition on stream communities (but see Molles 1982, Stout et al. 1992).

In this chapter, we compared aquatic macroinvertebrate community structure and composition in streams draining hemlock and mixed hardwood forests in an effort to predict long-term consequences of hemlock decline due to hemlock woolly adelgid (HWA). Orwig and Foster (1998) found stands suffering severe HWA-induced mortality in Connecticut showed little hemlock regeneration because small trees were disproportionately affected by HWA, and predicted a succession to mixed hardwood in affected stands. In addition, many of the hardwood-dominated catchments in Delaware Water Gap National Recreation Area (DEWA), particularly in ravine environments, were once hemlock but were replaced by mixed hardwoods following logging over 100 years ago (Sullivan et al. 1998). Therefore, we believe long-term predictions based on this comparative study reflect realistic assumptions regarding long-term changes in forest composition due to HWA. The specific mechanisms by which hemlock influences biological structure of both fish and aquatic invertebrates are explored in Chapter 4.

METHODS

Collection of Invertebrate Samples

We used the landscape-based, stratified pair sampling design described in Chapter 1 to select sites for collecting aquatic invertebrate samples. Invertebrate sampling was conducted during the first two weeks of April 1997 prior to spring emergence when benthic diversity is typically highest in small streams (Resh and McElravy 1993). Samples from streams of each hemlock/hardwood site pair were collected either on the same day or only one day apart to control for temporal differences in community structure. Sample reaches were defined by a distance of 80 meters for 1st order streams and 160 meters for 2nd order streams. These distances were selected because, on average, they represented approximately 40 mean stream widths and encompassed a minimum of three riffle-pool sequences in DEWA. Such areas have been found to be sufficient for measuring fish diversity (Lyons 1992, Angermeier and Smoger 1995) and consequently should be more than adequate for benthic invertebrates.

Two approaches were used for invertebrate sampling. Firstly, random sampling was used to obtain unbiased estimates of actual and relative abundances. A total of 20 equally spaced transects perpendicular to stream flow were established (i.e., 4 meters apart for the 80 meter 1st order reaches, and 8 meters apart for the 160 meter 2nd order reaches). At each transect, stream width was measured to the nearest 0.3 meters (i.e., opening of the standard D-frame kick net used in sampling) for all transects. Subsequently, a random number was generated between 0 and the stream width in 0.3 meter units using either a random number table or calculator. This number was rounded up and used to determine the location of a single sample site along each of the 20 transects. Sampling consisted of 30-second kicks with a standard D-frame kick net (net mesh = 250 microns) over an area of 0.09 m^2 at each selected site. All 20 samples were initially composited in 5-gallon buckets, and upon completion, placed into as many 1-liter nalgene sample jars as needed. Samples were preserved with 80% isopropyl alcohol in the field. Composite samples allowed us to maximize sampling effort among, as well as within, streams at the expense of assessing within-stream variability. Since we were interested in comparing biological structure among stream types, as opposed to reaches within a single stream, we believe composite sampling was justified.

Secondly, a qualitative, microhabitat-based approach was used to maximize the probability of collecting individuals of all species by ensuring sampling was conducted in all available microhabitats independent of their rarity. Available microhabitats were defined by combinations of water depth, velocity, substrate, and turbulence (Table 2-1). Two investigators (1 on each bank) searched the entire stream reach for the presence of each of the 50 possible microhabitat types. Attempts were made to collect a minimum of two samples from each available microhabitat type. Qualitative samples were also collected with a D-frame kick net. Every effort was also made to sample each microhabitat type well. This did not mean equal time because some microhabitat types were much easier to sample than others. For example, microhabitat types with leaf pack substrates required little time because leaf packs could be quickly removed and placed into the collecting net. Identity and number of all microhabitat types were also recorded. Resulting samples were composited as described above for random samples.

Table 2-1. Microhabitat matrix used to stratify qualitative sampling. Checked boxes refer to microhabitat types observed in DEWA streams.

Substrate	Slow-water habitats		Fast-water habitats		
	Depth <30 cm	Depth >30 cm	Fast/ turbulent	Fast/non- turbulent	Water falls
Logs (>30 cm)		X			
Sticks (<30 cm)	X		X	X	
Leaf packs	X		X	X	
Needle packs	X		X	X	
Moss	X		X	X	X
Silt/detritus (Not mineral)	X				
Sand (mineral: <pea sized)	X				
Gravel (mineral:pea-golf ball-sized)	X		X	X	X
Cobble (mineral golf ball-head-sized)	X	X	X	X	
Boulder/bedrock (mineral:>head-sized)	X	X	X	X	X

Laboratory Processing of Invertebrate Samples

Processing samples consisted of three phases: 1) a washing/floating phase designed to eliminate larger debris from the sample and separate the sample into organic and mineral fractions for easier picking (i.e., removing organisms from debris); 2) a subsampling phase designed to partition the composite samples into smaller units; and 3) the actual picking and preservation of invertebrates from remaining debris. Each of these phases is described in detail below:

Washing/floating phase. Initially, samples were poured into a large pan and the larger leaves and stones washed over a 250 micron sieve. Washed stones and leaves were returned to sample containers and preserved. A percentage of the resulting stone-leaf fractions were examined for missed insects to determine the efficiency of the washing phase (i.e., number of invertebrates found in stone-leaf fraction following washing relative to the total number of invertebrates found in the entire sample; mean observed efficiency was 85%). Invertebrates and smaller material

retained by the sieve were floated with a stream of water to separate invertebrates and organic debris from mineral material. Completion of this task resulted in an organic fraction that contained finer particulate organic matter and most of the invertebrates, and a mineral fraction containing largely sand, gravel, and some of the heavier invertebrates such as case-making caddisflies. Both organic and mineral fractions were subsequently subsampled as described below prior to picking.

Subsampling Phase. Composite samples contained huge numbers of individuals and so only a portion of each sample could be picked for identification. Consequently, some method of partitioning each sample into equal portions, and randomly selecting subsamples for picking was required. To do this, we fabricated a device that splits a sample into two equal fractions (by volume). The sample splitter consists of hinged bucket, a wedge, and two receiving receptacles. For each sample, the mineral and organic fractions were split separately as follows: Fractions were placed into the pouring bucket, the buckets tipped over the wedge, and the two subsamples collected. Each fraction was split into 16 subsamples and four of them (i.e., 25% of the total) were selected at random to pick. The 25% was chosen based on the results of a power analysis conducted on preliminary samples (i.e., the organic and mineral fraction from two samples). The power analysis was conducted for the total number of taxa and total number of individuals using a boot-strapping method of randomization (Manly 1991). We wrote a computer algorithm in S-Plus (Venables and Ripley 1994) that randomly drew a number of subsamples (one, two, four or eight) from the total (N=16), calculated the value of the response variable, and compared it to the true value from the entire sample. This process proceeded for at least 100 iterations and a distribution of differences was generated from the difference between the response from boot-strapped subsamples and that of the total sample. Using this approach, we found that data generated from four randomly selected subsamples (i.e., 1/4 of the total composite sample) was representative of the entire sample in terms of taxa richness and total abundance. That is, species richness and total abundance in the four subsamples was within 10% of that in the entire sample at least 95% of the time.

Picking and Preservation. Selected subsamples were picked in white enamel pans under a 1.25X magnifying lamp. Invertebrates and the remaining debris were preserved separately in 50% isopropyl alcohol. A fourth of the debris samples (n=14) were re-examined to determine efficiency during the picking phase (mean=91%). Where possible, all invertebrates were identified to the species level using appropriate keys. Count data from both mineral and organic fractions were then pooled for each sample and tabulated. A voucher collection was also created.

Data Summarization

A total of 184 taxa were positively identified from benthic samples; 85 taxa were identified to species, 90 to genus, 8 to family and 1 to order (Appendix 2-A, in this document and on attached diskette). However, as is typical with benthic samples, there were many uncertainties that forced us to edit the invertebrate data set prior to analysis. For example, although there were many taxa that were positively identified to species, in many instances there were samples that contained individuals of the same genus, but for various reason (e.g., specimens too small or key

morphological features missing) we were unable to identify them to species. Thus, to prevent overestimating diversity we were forced to lump all such individuals, whether identified to species or genus, at the genus level. The alternative would have been to count those specimens identified to genus as a separate taxa from those identified to species. For example, individuals keyed to *Baetis sp.* may or may not have been *Baetis tricaudatis*. To count both as separate taxon could potentially overestimate diversity and confound our analyses. A similar convention was used at all taxonomic levels. Therefore, analyses designed to detect hemlock effects on diversity were conservative. That is, because we probably under-represented diversity in our analyses, there may have been a larger forest type effect on diversity than reported here. The resulting data set contained a total of 151 taxa that were used for all subsequent analyses.

Two primary data matrices were created from the invertebrate samples and used for analyses. For those analyses based on species abundances (e.g., density and relative abundance comparisons), we used the site by species abundance matrix generated from the random samples only (Appendix 2-B, attached diskette). For those analyses based on occurrence or richness of species, we created a presence-absence matrix using data from both the random and qualitative samples (Appendix 2-C, attached diskette).

Secondary matrices were derived from the two primary matrices described above to compare trophic and taxonomic composition. For taxonomic composition, the number of individuals (derived by collapsing the site by species abundance matrix) and number of species (derived by collapsing the site by species presence-absence matrix) were determined for each of the following six taxonomic groups: Ephemeroptera, Plecoptera, Trichoptera, midge larvae, other insect taxa, and non-insect taxa. Similarly, for trophic composition, number of individuals and number of species were determined for each of the ten trophic classes used by Merritt and Cummins (1996): shredder-chewer, shredder-detritivore, shredder-gouger, collector-filterer, collector-gatherer, scraper, macrophyte-piercer, predator-engulfer, predator-piercer, and parasite. This suite of groups was reduced to seven because 3 groups (i.e., shredder-gouger, macrophyte-piercer, and parasites) were either not represented, or represented by only a few individuals. However, many species have been found to use several feeding modes (Appendix 2-A). Thus, for a given taxon at a given site, the number of individuals and number of taxa were weighted by the number of trophic classes assigned to that species. For example, if a given taxon was assigned to both scraper and predator-engulfer trophic classes, then for each site the number of individuals in the abundance matrix or the number of species in the presence/absence matrix would be divided by 2. Subsequently, all values within a trophic class were summed to obtain the total number of individuals or species of a given trophic class.

Data Analysis

We compared four community structure and three community composition metrics between streams draining hemlock and those draining hardwood forests (Table 2-2). Making use of the stratified pair design (see Chapter 1), we tested the null hypothesis that the difference in each community structure metric between site pairs was equal to zero (i.e., $p > 0.1$). That is, for each metric, we calculated the difference between individual hemlock-hardwood site pairs by

subtracting the value measured in the hemlock site from that in the corresponding hardwood site. We used general linear modeling to 1) test whether mean differences between forest types varied among stream types, and 2) test whether mean differences between forest types was equal to zero. Differences tended to be normally distributed so no transformations were required prior to analysis.

Table 2-2. Biological response variables compared between streams draining hemlock and hardwood forests within DEWA.

Community Structure	
Taxa Richness	Total number of taxa
Shannon-Weiner Taxa Diversity Index	Metric that incorporates information on both taxa richness and the evenness with which taxa are distributed. Calculated as: $H'=-\sum p_i \log p_i$, where H'=Shannon Index, and p_i is the proportion of individuals occurring in taxon i.
Total Density	Total number of individuals per square meter.
Number of Rare Taxa	Rare taxa defined as those occurring at three sites or fewer.
Community Composition	
Trophic Composition	Proportion of taxa in each of the following seven trophic categories: shredder-chewers, shredder-detritivore, collector-filterer, collector-gatherers, scrapers, predator-engulfers, predator-piercers.
Taxonomic Composition	Proportion of taxa in each of the following six taxonomic categories: Ephemeroptera, Plecoptera, Trichoptera, Midges (i.e., Chironomidae), other insects, other non-insect taxa.
Taxa Occurrence	Proportion of sites in which each taxon occurs; calculated separately for each taxon.

We used multi-response permutation procedures (MRPP) to compare the proportion of taxa in each of the seven trophic and six taxonomic groups between streams draining hemlock and those draining hardwood forests. We also used MRPP to test for biological differences among the three terrain strata and two stream orders. For this analysis, we used proportions rather than count data to remove the effect of differences in taxa richness and focus on compositional differences. MRPP is a non-parametric procedure similar in purpose to discriminant analysis but has the advantage of not requiring multivariate normality and homogeneity of variance that are seldom met with ecological community data (McCune and Mefford 1995). Cases where the multivariate response was significant, we used the Kruskal-Wallis one-way ANOVA to test whether the proportion of individual trophic or taxonomic groups differed among forest or stream types.

We used logistic regression to conduct an odds ratio test that estimates the association between the occurrence of each taxon and forest type. The odds of taxon presence is the probability of presence divided by the probability of absence. There are two relevant odds: one specific to hemlock stands and the other specific to hardwood stands. The ratio of these odds is the odds ratio. The natural log of the odds ratio makes the statistic easily interpretable. In our case, log-odds ratio less than zero indicated taxa association with hardwood; whereas, ratios greater than zero indicate an association with hemlock. We computed odds ratios and p-values using LogXact (Mehta and Patel 1996).

Based on the results of the odds ratio test, we were interested in whether those taxa found to be associated with hemlock were a random subset of the community, or if they were taxonomically or functionally different. We used Fisher's Exact Test to test the hypothesis that trophic and taxonomic groups were equally represented among taxa associated with hemlock and those not associated with hemlock. We used StatExact (Mehta and Patel 1997) to calculate Fisher's test statistics and exact p-values.

RESULTS

Invertebrate Community Structure and Composition

We observed a significant forest type effect on all four community structure statistics examined. Overall, hemlock had a positive effect on total taxa richness and Shannon species diversity index, and a negative effect on total abundance and rare taxa richness (Fig. 2-1, pooled strata). Taxa richness was on average 37% higher in streams draining hemlock forests, and Shannon diversity index was about 9% higher on average. In contrast, streams draining hardwood forests supported an average of 42% more individuals (total density) than streams draining hemlock. Likewise, the number of rare species (i.e., those that occurred at fewer than 3 sites) were on average 67% more common in streams draining hardwood forest.

The significance and magnitude of the hemlock effect depended on stream type for species richness (ANOVA, F=3.265; df=4,9; p=0.065) and Shannon diversity index (F=3.905; df=4,9; p=0.042) but not for density and number of rare taxa (p>0.25 for both). However, for all four community structure metrics, 1st order, mid-slope sites responded differently than the other stream types, either showing no forest type effect , as with total richness, density, and rare taxa richness; or the opposite effect of the other stream types, as with Shannon diversity index (Fig. 2-1). Consequently, the pooled effect was examined with and without that stream type included. After removing 1st order mid-slope sites, the forest type effect (i.e., difference between site pairs) was no longer dependent on stream type for total taxa richness (F=2.426; df=3,7; p=0.151) or Shannon diversity index (F=1.417; df=3,7; p=0.316). Therefore, these results suggest a significant overall forest type effect on all four community structure metrics except in 1st order, mid-slope sites. Also, the fact 1st order mid-slope sites had significantly higher Shannon diversity in streams within hardwood forests but no difference in total richness between forest types suggests higher dominance in the hemlock sites for this stream type. That is, the distribution of individuals was less evenly distributed among species in the hemlock sites.
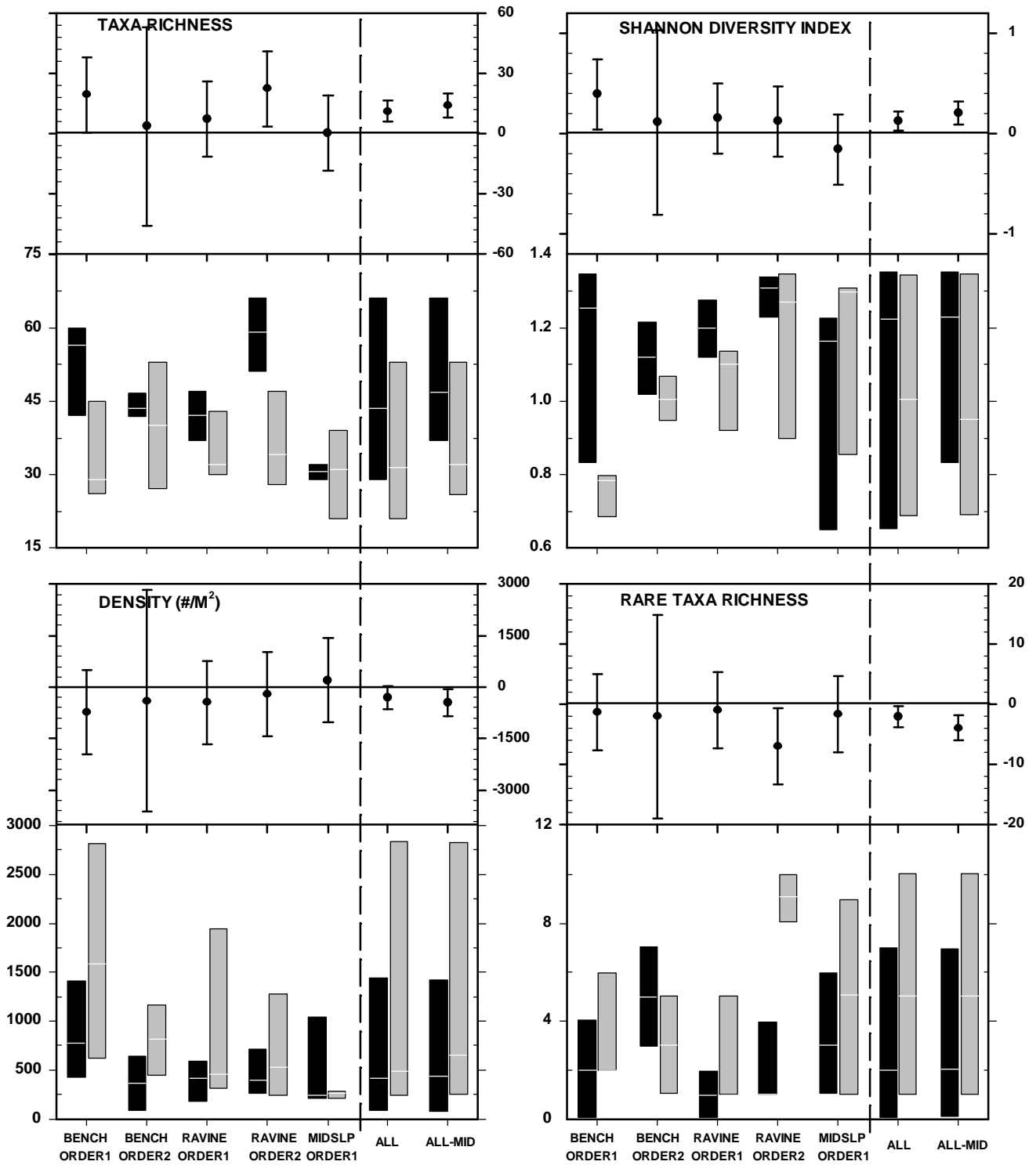
Figure 2-1. Comparison of four community structure metrics between streams draining hemlock and hardwood forests. Top panel shows mean differences (+/- 90% C.L.) between hemlock-hardwood site pairs. Positive values indicate higher means for hemlock. Bottom panel compares the range of values (limits of box) and medians (white 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).

2.8

More detailed comparisons of the composition of the invertebrate community revealed three important patterns. Firstly, trophic composition of the invertebrate community was significantly different between streams draining hemlock and hardwood forests as well as between the two stream orders (Table 2-3). Observed differences in trophic structure was not significant between terrain types. In streams draining hemlock, predator-engulfers represented a larger proportion and scrapers a smaller proportion of the invertebrate community in both 1st and 2nd order streams (Fig. 2-2). In contrast, taxonomic differences were only observed among terrain types (Table 2-3). Mayflies (Ephemeroptera) represented a larger proportion of the community in ravines, stoneflies (Plecoptera) in mid-slope sites, and midges in bench sites (Fig. 2-3). No hemlock effect on taxonomic composition was observed. These data indicate the higher taxonomic richness and diversity observed in streams draining hemlock were associated with distinct differences in trophic composition.

Table 2-3. Results of MRPP to test for proportional differences in trophic and taxonomic composition between forest type, terrain type, and stream order.

	Trophic Composition (7 groups)		Taxonomic Composition (6 groups)	
Stratum	MRPP statistic	P value	MRPP statistic	P value
Forest type (hemlock/hardwood)	-3.882	0.004	0.389	0.590
Terrain type (bench, ravine, mid-slope)	-1.322	0.102	-1.925	0.044
Stream order (1st, 2nd order)	-1.755	0.061	0.517	0.650

Secondly, a large number of taxa (n=15) occurred significantly more often in streams draining hemlock forests than those draining hardwood forests (i.e., strong hemlock associates, Fig. 2-4). Although 15 taxa may be within the range expected to show significant differences due to chance, the fact that all were associated with hemlock suggests forest type preferences. Of the 15 taxa, only three were found to occur only in streams draining hemlock (Table 2-4). However, the extent to which streams that drain hardwood forests contained strong hemlock associates seemed to be, in part, related to the proximity of the stream to hemlock. That is, the number of strong hemlock associates found in hardwood sites was inversely related to the distance to the nearest hemlock site, at least for a large fraction of the sites (Wald statistic:11.47, df=1, p=0.001; Fig. 2-5).
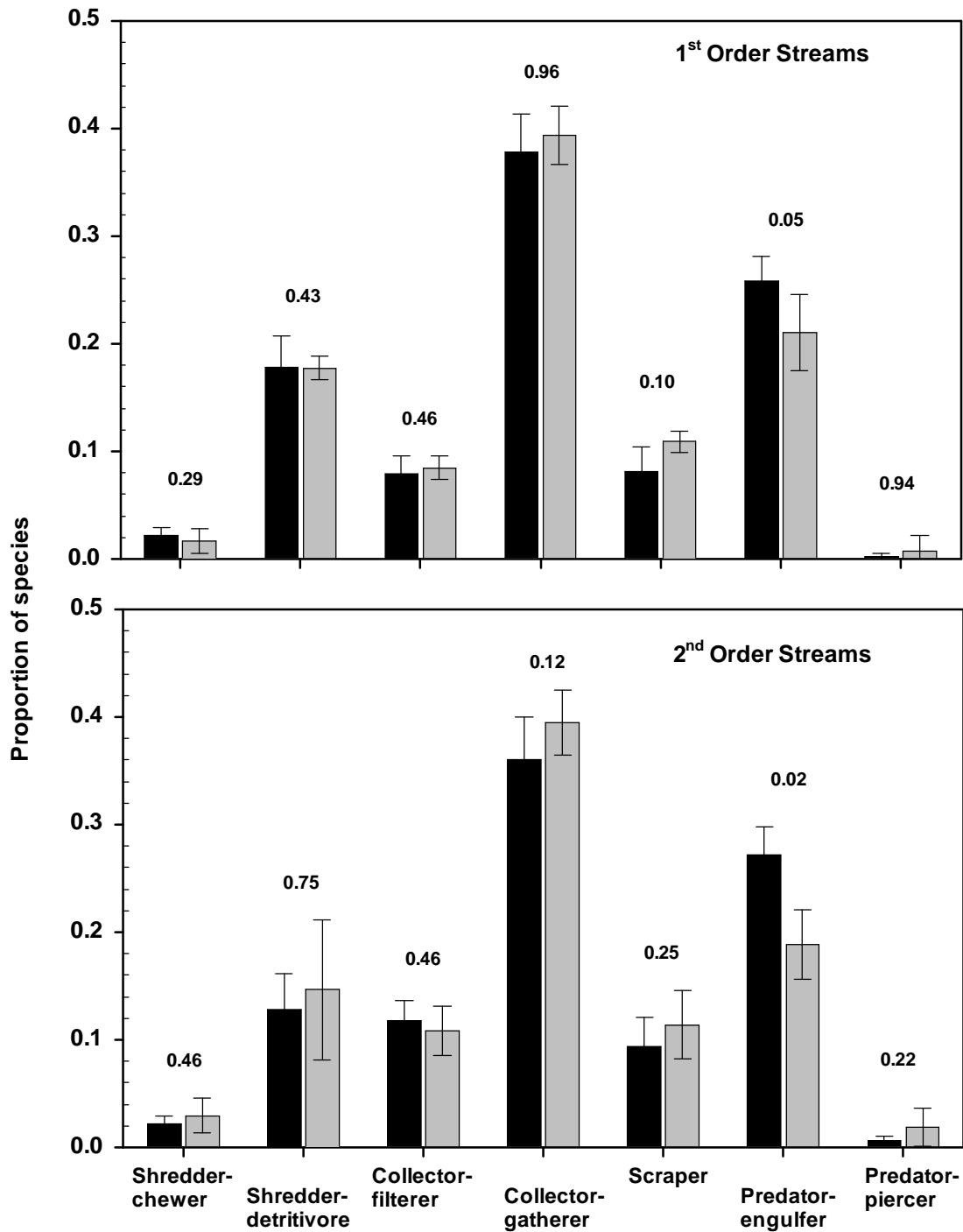
Figure 2-2. Comparison of stream invertebrate trophic structure between streams draining hemlock (black bars) and hardwood (gray bars) forests. Vegetation comparisons (mean proportion of species +/- 90% C. L.) are made within each stream order because stream order was also found to influence trophic composition (see text). No differences were observed among terrain types. Numbers above bars are p-values from Kruskal-Wallis one-way ANOVA with 2 d.f.
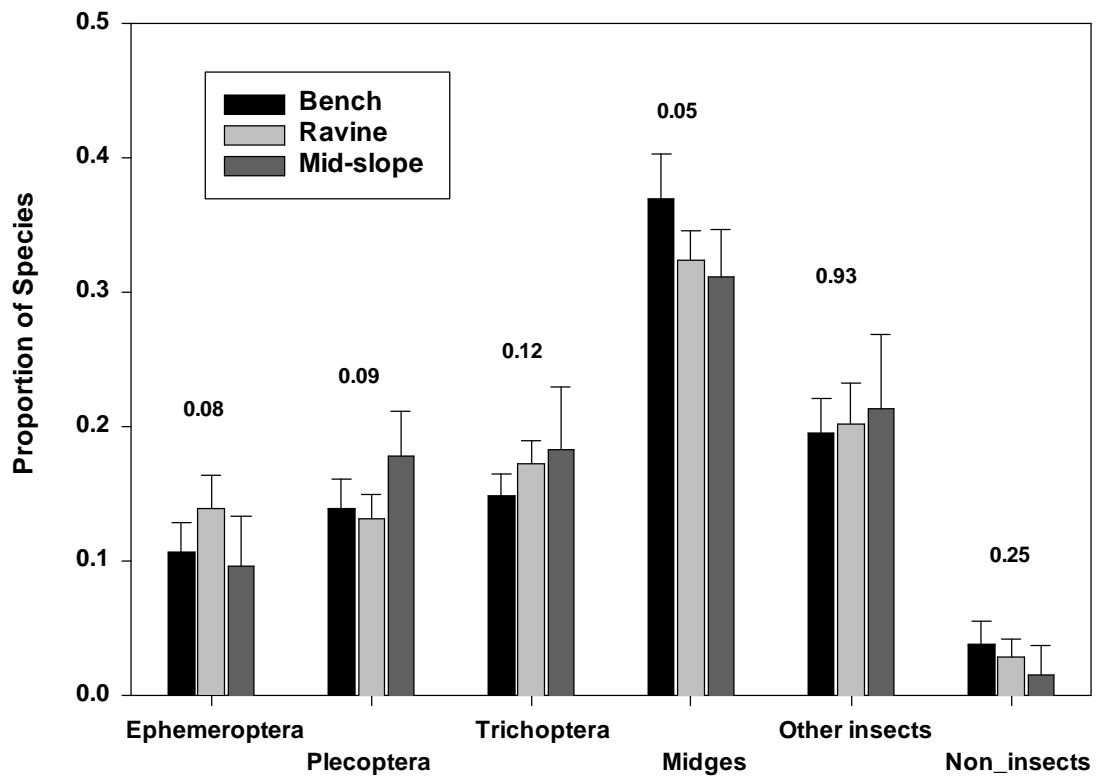
Figure 2-3. Comparison of stream invertebrate taxonomic composition between terrain types. No differences in taxonomic composition was observed between vegetation types or stream order (see text). Mean proportion of each taxa and associated 90% confidence limits are presented for each terrain type. Number above bars are p-values from Kruskal-Wallis one-way ANOVA with 2 df.
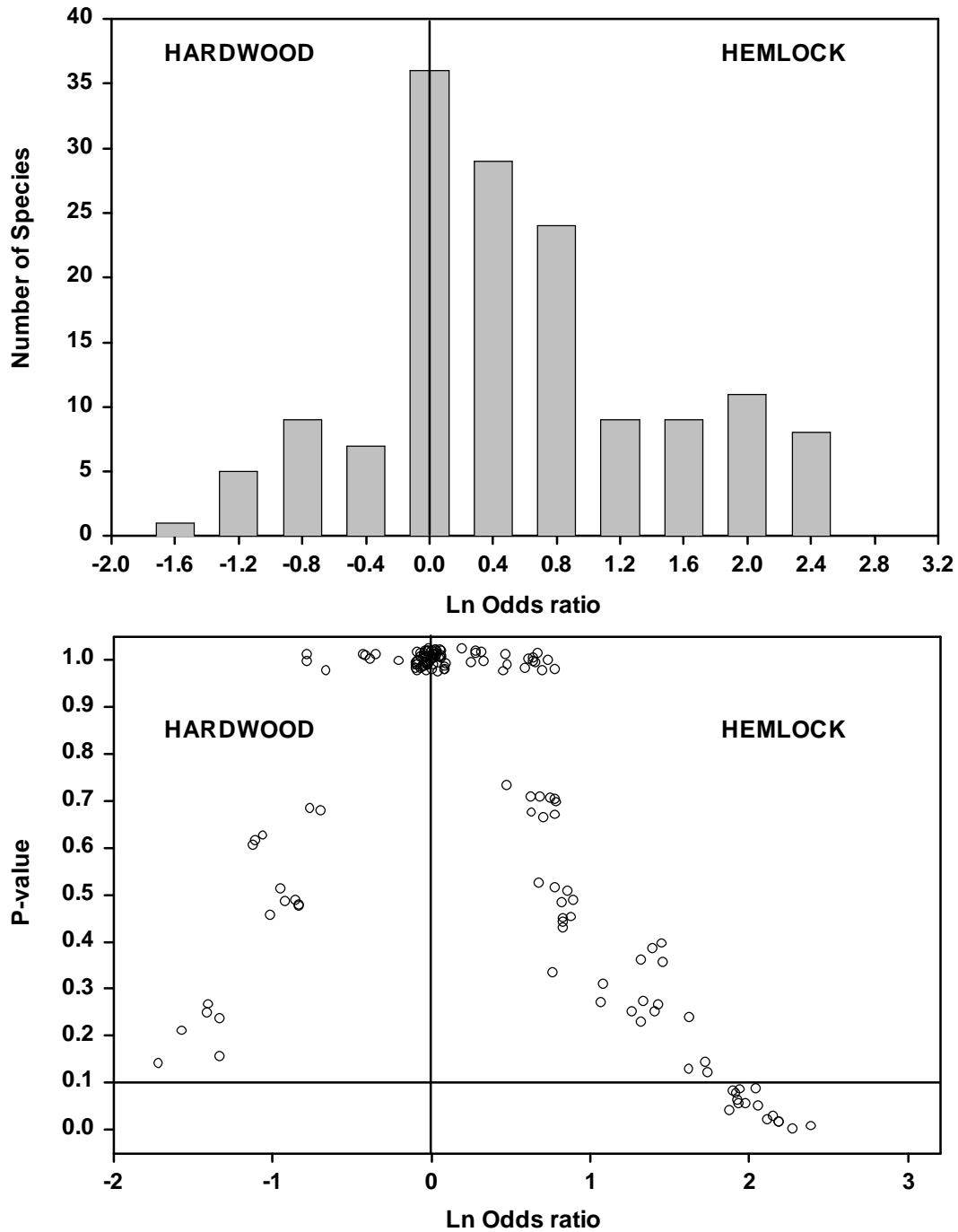
Figure 2-4. Results of odds ratio test to determine taxa-specific associations with vegetation types. For each taxa, ratio of occurrence in streams draining hemlock to that in hardwood was used and therefore positive values indicate a preference for hemlock. Top figure shows the distribution of species with various odds ratios. Bottom figure shows the significance (i.e., p-values) as a function of the odds ratio. A random jitter function was applied to data to enhance visual separation.

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Table 2-4. Identity of taxa with forest type preferences. Strong preference defined as p-values of less than 0.1 in odd ratio test (see Methods). Weak preferences defined as p-values less than 0.30. *indicates taxa found only in streams draining hemlock.

| Taxon	Taxonomic Class	Trophic Class
Strong Hemlock Assoc.		
Eurylophella sp.	Ephemeroptera	Collector-gatherer
Leptophlebiidae	Ephemeroptera	Collector-gatherer; shredder-detritivore
Lanthus parvulus	Other Insect (Odonata)	Predator-engulfer
Leuctra sp.	Plecoptera	Shredder-detritivore
Perlidae	Plecoptera	Predator-engulfer
Hydropsyche ventura	Trichoptera	Collector-filterer
Lepidostoma sp.	Trichoptera	Shredder-detritivore
Polycentropus sp.	Trichoptera	Predator-engulfer, collector-filterer
Bezzia sp.	Other Insect (Diptera)	Predator-engulfer
Brillia sp.	Midge	Shredder-chewer, collector-gatherer
Natarsia sp.	Midge	Predator-engulfer
Polypedilum sp.	Midge	Collector-gatherer; predator-engulfer
Rheocricotopus sp.	Midge	Collector-gatherer; shredder-detritivore
Hexatoma sp.	Other Insect (Diptera)	Predator-engulfer
Pseudolimnophila sp.	Other Insect (Diptera)	Predator-engulfer
Weak Hemlock Assoc.		
Adicrophleps hitchcocki	Trichoptera	Shredder-detritivore
Limnephilidae	Trichoptera	Shredder-detritivore
Rhyacophila minora	Trichoptera	Predator-engulfer
Promoresia sp.	Other Insect (Coleoptera)	Scraper
Georthocladium sp.	Midge	Collector-gatherer
Psilometriocnemus sp.	Midge	Collector-gatherer
Symbiocladius sp.	Midge	Collector-gatherer
Dolichopodidae	Other Insect (Diptera)	Predator-engulfer
Molophilus sp.	Other Insect (Diptera)	Collector-gatherer
Pisidium sp.	Non-insect (Mollusca)	Scraper
Weak Hardwood Assoc.		
Allocapnia sp.	Plecoptera	Shredder-detritivore
Prostoia similis	Plecoptera	Shredder-detritivore
Chaetocladius sp.	Midge	Collector-gatherer
Diplocladius sp.	Midge	Collector-gatherer
Clinocera sp.	Other Insect (Diptera)	Predator-engulfer
Tipula sp.	Other Insect (Diptera)	Shredder-detritivore
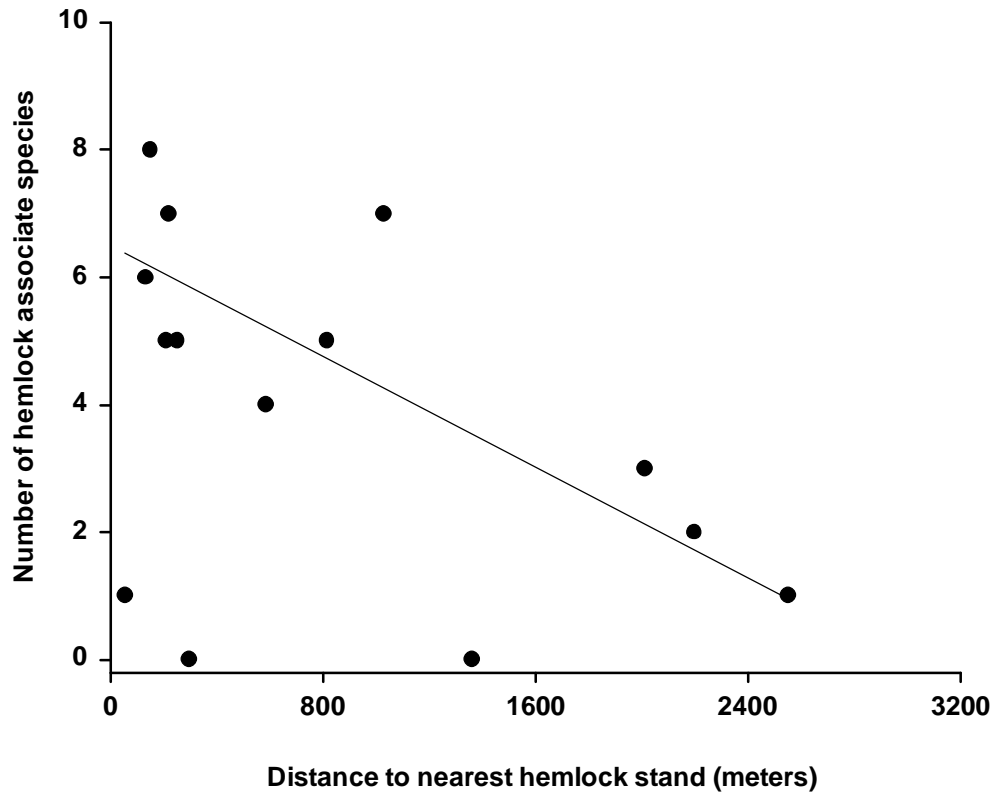
Figure 2-5. Relationship between the number of strong hemlock associates observed in streams draining hardwood forests, as a function of distance to the nearest hemlock stand. Regression line fitted using Robust Regression (Ryan 1997) which reduces the influence of outliers.

Finally, we compared the trophic and taxonomic composition of the 25 hemlock associates (strong and weak) described above to the rest of the community to see whether they represented a random subset of the community or if they were taxonomically or functionally different. We found taxa in the hemlock associate group to be distributed differently among the seven trophic groups (Fishers Exact Test, χ^2=9.68, p=0.09) than taxa in the rest of the community. More specifically, we found a significantly larger fraction of predator-engulfer taxa and a significantly smaller fraction of scraper taxa in the hemlock associate group (Fig. 2-6). The pattern was even more pronounced if only strong hemlock associates were included. Also, the proportion of collector-gatherer taxa were marginally lower and the proportion of shredder-detritivore were marginally higher in the hemlock associate group. We observed no differences in composition among the six taxonomic groups (Fishers Exact Test, χ^2=2.60, p=0.78), though results for Trichoptera were marginal (Fig. 2-6).
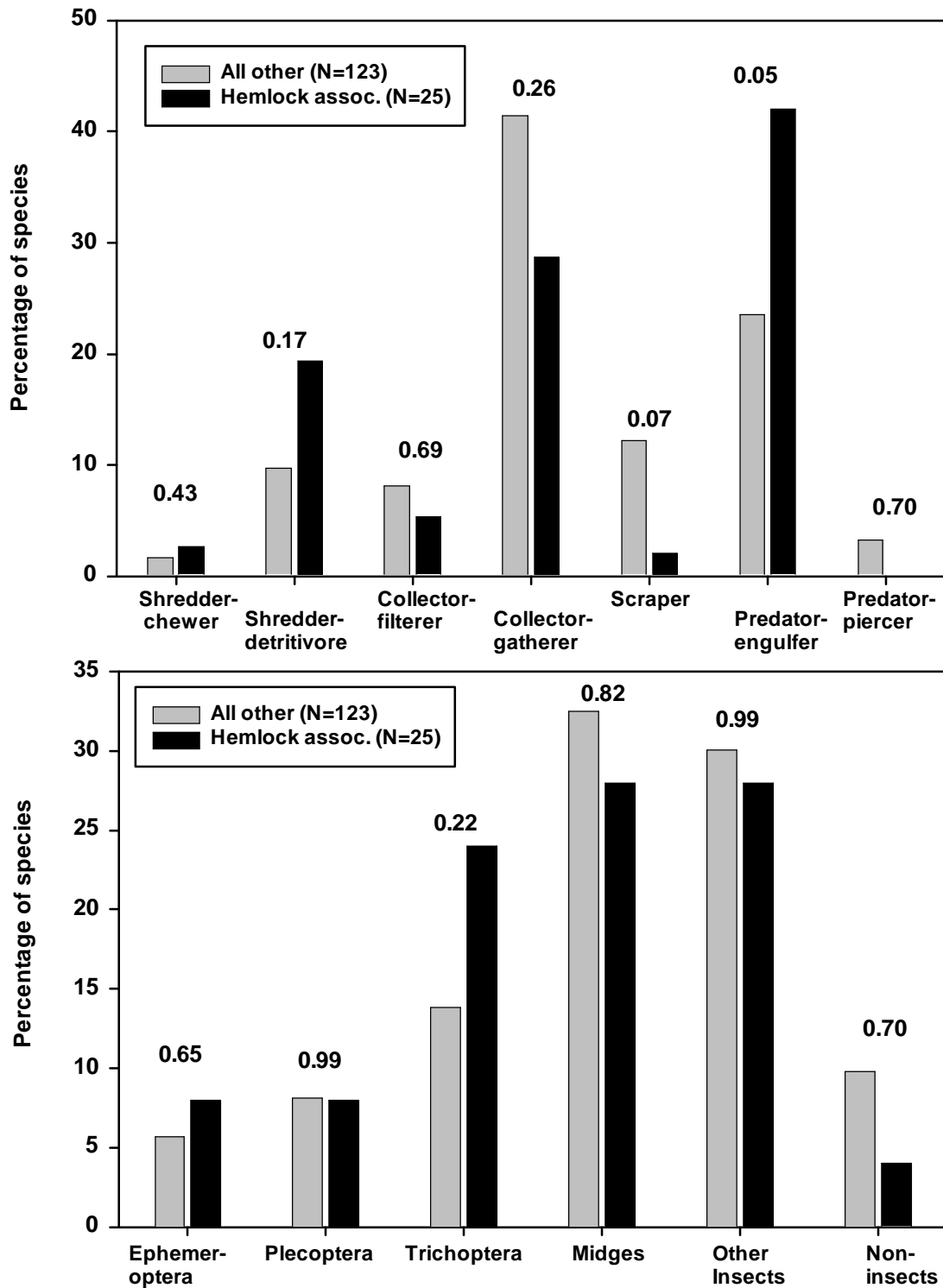
Figure 2-6. Comparison of trophic (top) and taxonomic (bottom) composition between the 25 hemlock associates and the 123 other taxa. Numbers at the top of each pair of bars are p-values resulting from a series of 2X2 Fisher's Exact Tests that test for differences between forest types for each trophic and taxonomic group. Results of the overall contingency tests on the distribution of trophic and taxonomic composition between vegetation types are reported in the text.

DISCUSSION

We found significant differences in all four invertebrate community structure metrics examined between streams draining hemlock and those draining hardwood forests for most stream types. Taxa richness and diversity were higher in hemlock while total density and rarity were lower. First order, mid-slope sites deviated from this pattern for all metrics examined (Fig. 2-1). We believe the steep slope associated with this stream type (Fig. 1-3) reduced residence time of water and nutrients within any particular reach of stream and consequently reduced the time with which forest influences could act. Streams in ravine environments also had steep slopes (Fig. 1-3), but were characterized by a more stair-step profile, with relatively long, low-gradient reaches punctuated by large waterfalls. Consequently, residence time of water and nutrients in ravines may be longer. Geomorphic characteristics including slope and valley shape have long been known to influence biological structure of stream communities and their responses to disturbance (Naiman et al. 1992), and they are the basis for most contemporary stream classification systems (e.g., Rosgen 1985, Frissel et al. 1986, Hawkins et al. 1993).

In addition, we found about 10% (N=15) of all invertebrate taxa collected occurred significantly more often in streams draining hemlock (Fig. 2-4), and that these hemlock associates were not a random subset of the community, but rather had a trophic composition distinct from the rest of the community (Fig. 2-6). Specifically, the proportion of predators was higher and the proportion of grazing algivores was lower in "hemlock associates" than the rest of the community. An additional 7% (N=10) showed a weaker preference for hemlock. Furthermore, these taxa showed a relatively strong association with hemlock even where they occurred in streams draining hardwood forests (Fig. 2-5). Specifically, the number of "strong hemlock associates" in hardwood sites correlated with the proximity of those streams to hemlock stands. Two streams draining hardwood had few or no hemlock associates despite their relative proximity to hemlock (Fig. 2-5). This suggests that, in addition to proximity to hemlock stands, other factors such as the size of the nearest hemlock stand, the number of hemlock stands nearby, the amount of stream habitat within hemlock stands, and/or stochastic factors related to dispersal and distribution may also be important. Nevertheless, the fact that there were no sites distant from hemlock stands that supported large number of "hemlock associates" further supports the argument that hemlock, or stream conditions induced by hemlock, are important to these species. This pattern is consistent with a source-sink model whereby individuals frequently disperse from hemlock sites to hardwood sites, but the survival and/or reproductive capacity of these immigrants is compromised. Thus, despite the occurrence of many of these taxa in hardwood sites, habitat conditions in streams draining hardwood forests may not be sufficient to sustain these taxa over the long term in the absence of hemlock. Dispersal patterns of aquatic insects are poorly understood and the relationship of aquatic insect dispersal with productivity, disturbance patterns, and habitat conditions has not been determined for most taxa (Sheldon 1984). Vegetation-induced differences in stream habitat conditions that cause the biological differences we observed will be explored in Chapter 4.

Whatever the proximate cause, it is clear that streams draining hemlock forests represent "hot spots" of diversity within DEWA. If the distribution and abundance of hemlock forests are compromised by HWA, we would predict a significant decline in both alpha (within site) and gamma (park-wide) aquatic invertebrate diversity. Declines in invertebrate diversity might also be expected to cascade to other assemblages, both aquatic (e.g., fish) and terrestrial (e.g., insectivorous birds and mammals), throughout the watershed.

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Appendix 2-A. List of taxa positively identified from DEWA samples and their respective trophic classification. Trophic classes were derived from Merrit and Cummins (1996) and are as follows: SC=shredder-chewer; SD=shredder-detritivore; SG=shredder-gouger; CF=collector-filterer; CG=collector-gatherer; S=scraper; MP=macrophyte piercer; PE=predator-engulfer; PP=predator-piercer; and PA=parasites.

Phylum	Class	Order	Family	Genus/Species	Trophic
Annelida	Oligochaeta	Haplotaxida	Megascolecidae		CG
Annelida	Oligochaeta	Lumbricida	Lumbricidae		CG
Annelida	Oligochaeta	Lumbriculida	Lumbriculidae	Lumbriculus variegatus	CG
Annelida	Oligochaeta	Tubificida	Enchytraeidae		CG
Annelida	Oligochaeta	Tubificida	Tubificidae	Spirosperma nikolskyi	CG
Arthropoda	Arachnida	Acariformes	Hydryphantidae		PE,PA
Arthropoda	Arachnida	Acariformes	Torrenticolidae	Torrenticola sp.	PE,PA
Arthropoda	Crustacea	Amphipoda	Crangonyctidae	Stegonectes sp.	CG,SD,PE
Arthropoda	Crustacea	Decapoda	Cambaridae		CG,SD,PE
Arthropoda	Insecta	Collembola	Hypogastruridae	Xynella sp.	CG
Arthropoda	Insecta	Collembola	Isotomidae	Agrenia sp.	CG
Arthropoda	Insecta	Ephemeroptera	Ameletidae	Ameletus sp.	S,CG
Arthropoda	Insecta	Ephemeroptera	Baetidae	Acerpenna pygmaea	CG
Arthropoda	Insecta	Ephemeroptera	Baetidae	Baetis tricaudatus	CG,S
Arthropoda	Insecta	Ephemeroptera	Baetidae	Baetis sp. (two-tail)	CG,S
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Ephemerella dorothea	CG,S
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Ephemerella rotunda	CG,S
Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Eurylophella funeralis	CG
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Epeorus (Iron) sp.	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Rhithrogena sp.	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema meririvulanum	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema pudicum	CG,S
Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema vicarium	CG,S
Arthropoda	Insecta	Ephemeroptera	Isonychiidae	Isonychia sp.	CF
Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae	Paraleptophlebia sp.	CG,SD
Arthropoda	Insecta	Odonata	Aeschnidae	Boyeria vinosa	PE
Arthropoda	Insecta	Odonata	Coenagrionidae	Ischnura sp.	PE
Arthropoda	Insecta	Odonata	Cordulegasteridae	Cordulegaster sp.	PE
Arthropoda	Insecta	Odonata	Gomphidae	Lanthus parvulus	PE
Arthropoda	Insecta	Plecoptera	Capniidae	Allocapnia sp.	SD
Arthropoda	Insecta	Plecoptera	Capniidae	Paracapnia sp.	SD
Arthropoda	Insecta	Plecoptera	Chloroperlidae	Sweltsa sp.	PE
Arthropoda	Insecta	Plecoptera	Leuctridae	Leuctra sibleyi	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Amphinemura delosa	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Amphinemura wui	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Paranemoura perfecta	SD
Arthropoda	Insecta	Plecoptera	Nemouridae	Prostoia similis	SD
Arthropoda	Insecta	Plecoptera	Peltoperlidae	Tallaperla sp.	SD
Arthropoda	Insecta	Plecoptera	Perlidae	Agnetina capitata	PE
Arthropoda	Insecta	Plecoptera	Perlidae	Acroneuria abnormis	PE
Arthropoda	Insecta	Plecoptera	Perlidae	Acroneuria carolinensis	PE

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Plecoptera	Perlodidae	Malirekus iroquois	PE
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	Pteronarcys biloba	SD
Arthropoda	Insecta	Plecoptera	Pteronarcyidae	Pteronarcys proteus	SD
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	Bolotoperla rossi	SD
Arthropoda	Insecta	Plecoptera	Taeniopterygidae	Oemopteryx contorta	SD
Arthropoda	Insecta	Hemiptera	Corixidae	Hesperocorixa sp.	MP
Arthropoda	Insecta	Megaloptera	Corydalidae	Nigronia fasciatus	PE
Arthropoda	Insecta	Megaloptera	Corydalidae	Nigronia serricornis	PE
Arthropoda	Insecta	Megaloptera	Sialidae	Sialis sp.	PE
Arthropoda	Insecta	Trichoptera	Brachycentridae	Adicrophleps hitchcocki	SD
Arthropoda	Insecta	Trichoptera	Brachycentridae	Micrasema sprulesi	SD,SC
Arthropoda	Insecta	Trichoptera	Glossosomatidae	Glossosoma sp.	S
Arthropoda	Insecta	Trichoptera	Hydroptilidae	Palaeagapetus celsus	SD
Arthropoda	Insecta	Trichoptera	Hydroptilidae	Hydroptila sp.	MP,S
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Cheumatopsyche sp.	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Diplectrona modesta	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Hydropsyche sparna	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Hydropsyche ventura	CF
Arthropoda	Insecta	Trichoptera	Hydropsychidae	Parapsyche apicalis	CF
Arthropoda	Insecta	Trichoptera	Lepidostomatidae	Lepidostoma sp.	SD
Arthropoda	Insecta	Trichoptera	Limnephilidae	Ironoquia sp.	SD
Arthropoda	Insecta	Trichoptera	Limnephilidae	Pycnopsyche sp.	SD
Arthropoda	Insecta	Trichoptera	Molannidae	Molanna blenda	S,CG,PE
Arthropoda	Insecta	Trichoptera	Odontoceridae	Psilotreta frontalis	S,CG
Arthropoda	Insecta	Trichoptera	Philopotamidae	Dolophilodes distinctus	CF
Arthropoda	Insecta	Trichoptera	Polycentropodidae	Polycentropus sp.	PE,CF,SD
Arthropoda	Insecta	Trichoptera	Psychomyiidae	Lype diversa	S
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila fuscula	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila glaberrima	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila minora	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila nigrita	PE
Arthropoda	Insecta	Trichoptera	Rhyacophilidae	Rhyacophila torva	PE
Arthropoda	Insecta	Trichoptera	Uenoidae	Neophylax concinnu	S
Arthropoda	Insecta	Trichoptera	Uenoidae	Neophylax nacatus	S
Arthropoda	Insecta	Lepidoptera			SD,S
Arthropoda	Insecta	Coleoptera	Curculionidae		SC
Arthropoda	Insecta	Coleoptera	Dryopidae	Helichus sp.	SD
Arthropoda	Insecta	Coleoptera	Elateridae	Megapenthes sp.	CG
Arthropoda	Insecta	Coleoptera	Elmidae	Macronychus glabratus	CG
Arthropoda	Insecta	Coleoptera	Elmidae	Oulimnius latiusculus	CG,S
Arthropoda	Insecta	Coleoptera	Elmidae	Promoresia tardella	CG,S
Arthropoda	Insecta	Coleoptera	Haliplidae	Peltodytes lengi	PP,SD,PE

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Coleoptera	Psephenidae	Ectopria nervosa	S
Arthropoda	Insecta	Coleoptera	Psephenidae	Psephenus herricki	S
Arthropoda	Insecta	Diptera	Blephariceridae	Blepharicera sp.	S
Arthropoda	Insecta	Diptera	Ceratopogonidae	Bezzia/Palpomyia sp.	PE
Arthropoda	Insecta	Diptera	Ceratopogonidae	Ceratopogon sp.	PE
Arthropoda	Insecta	Diptera	Ceratopogonidae	Probezzia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Brillia flavifrons	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Brillia parva	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Brillia sera	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Brundiniella sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Chaetocladius dentiforceps	CG
Arthropoda	Insecta	Diptera	Chironomidae	Chaetocladius piger	CG
Arthropoda	Insecta	Diptera	Chironomidae	Conchapelopia sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Constempellina sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Corynoneura sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Cricotopus bicinctus	SC,CG
Arthropoda	Insecta	Diptera	Chironomidae	Diamesa sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Diplocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Doithrix sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella brehmi	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella brevicalcar	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella claripennis	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella devonica	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella gracei	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella pseudomontana	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Eukiefferiella rectangularis	CG,S,PE
Arthropoda	Insecta	Diptera	Chironomidae	Georthocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Heleniella sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Heterotrissocladius hirtapex	CG
Arthropoda	Insecta	Diptera	Chironomidae	Hydrobaenus sp.	S,CG
Arthropoda	Insecta	Diptera	Chironomidae	Limnophyes sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Larsia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Meropelopia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Micropsectra sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Microtendipes pedellus	CF
Arthropoda	Insecta	Diptera	Chironomidae	Nanocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Natarsia baltimorea	PE
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius clarkei	CG
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius dorenus	CG
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius mallochi	CG
Arthropoda	Insecta	Diptera	Chironomidae	Orthocladius obumbratus	CG
Arthropoda	Insecta	Diptera	Chironomidae	Parametriocnemus sp.	CG

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Diptera	Chironomidae	Paratendipes sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Paratrichocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Polypedilum aviceps	SC,CG,PE
Arthropoda	Insecta	Diptera	Chironomidae	Polypedilum illinoense	SC,CG,PE
Arthropoda	Insecta	Diptera	Chironomidae	Polypedilum tritum	SC,CG,PE
Arthropoda	Insecta	Diptera	Chironomidae	Pseudorthocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Pseudosmittia sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Psilometriocnemus sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Rheocricotopus eminellobus	CG,SC,PE
Arthropoda	Insecta	Diptera	Chironomidae	Rheocricotopus tuberculatus	CG,SC,PE
Arthropoda	Insecta	Diptera	Chironomidae	Rheopelopia sp.	PE
Arthropoda	Insecta	Diptera	Chironomidae	Rheosmittia sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Rheotanytarsus sp.	CF
Arthropoda	Insecta	Diptera	Chironomidae	Stempellina sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Stempellinella sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Stenochironomus sp.	CG,SG
Arthropoda	Insecta	Diptera	Chironomidae	Stilocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Synorthocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Tanytarsus sp.	CF
Arthropoda	Insecta	Diptera	Chironomidae	Thienemanniella sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Tribelos jucundus	CG
Arthropoda	Insecta	Diptera	Chironomidae	Trissocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Trissocladius sp.	CG
Arthropoda	Insecta	Diptera	Chironomidae	Tvetenia bavarica	CG
Arthropoda	Insecta	Diptera	Chironomidae	Zavrelimyia sp.	PE
Arthropoda	Insecta	Diptera	Dixidae	Dixa sp.	CG
Arthropoda	Insecta	Diptera	Dolichopodidae	Medetera sp.	PE
Arthropoda	Insecta	Diptera	Empididae	Chelifera sp.	PE
Arthropoda	Insecta	Diptera	Empididae	Clinocera sp.	PE
Arthropoda	Insecta	Diptera	Empididae	Oreogeton sp.	PE
Arthropoda	Insecta	Diptera	Rhagionidae	Chrysopilus sp.	PP
Arthropoda	Insecta	Diptera	Sciaridae	Corynoptera sp.	CG
Arthropoda	Insecta	Diptera	Simuliidae	Prosimulium arvum	CF
Arthropoda	Insecta	Diptera	Simuliidae	Stegopterna mutata	CF
Arthropoda	Insecta	Diptera	Simuliidae	Simulium vittatum	CF
Arthropoda	Insecta	Diptera	Stratiomyidae		CG
Arthropoda	Insecta	Diptera	Tabanidae	Chrysops sp.	PP
Arthropoda	Insecta	Diptera	Tabanidae	Tabanus sp.	PP
Arthropoda	Insecta	Diptera	Tipulidae	Antocha sp.	SD
Arthropoda	Insecta	Diptera	Tipulidae	Dicranota sp.	PE
Arthropoda	Insecta	Diptera	Tipulidae	Erioptera sp.	CG
Arthropoda	Insecta	Diptera	Tipulidae	Hexatoma sp.	PE

Appendix 2-A (continued).

Phylum	Class	Order	Family	Genus/Species	Trophic
Arthropoda	Insecta	Diptera	Tipulidae	Pedicia sp.	PE
Arthropoda	Insecta	Diptera	Tipulidae	Pilaria sp.	PE
Arthropoda	Insecta	Diptera	Tipulidae	Pseudolimnophila sp.	PE,SD
Arthropoda	Insecta	Diptera	Tipulidae	Tipula sp.	SD
Arthropoda	Insecta	Diptera	Syrphidae		CG
Mollusca	Gastropoda	Basommatophora	Planorbidae	Gyraulus parvus	S
Mollusca	Gastropoda	Basommatophora	Physidae	Physella sp.	S
Mollusca	Pelecypoda	Eulamellibranchia	Sphaeriidae	Pisidium casertanum	CG