

Role of rarity and taxonomic resolution in a regional and spatial analysis of stream macroinvertebrates

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Abstract. Quantitative sampling of benthic macroinvertebrate communities from 60 sites in New York City's drinking-water-supply watersheds was undertaken in 2000, 2001, and 2002 as part of a large-scale enhanced water-quality monitoring project (the Project). Sampling yielded 543 macroinvertebrate taxonomic units, most of which (including Chironomidae) were identified to the genus/species level. Our goals were to investigate the effect of level of taxonomic resolution on statistical macroinvertebrate–environment relationships, the effect of including rare taxa on among-site similarity and macroinvertebrate–environment relationships, and the correlations between the common and rare components of the total community at each site. Mean site richness ranged from 90.8 to 101.2 taxa for sites west of Hudson River (WOH) and 62.2 to 78.5 taxa for sites east of Hudson River (EOH). Species-level identifications provided the greatest separation of sites in multivariate space, but genus- and family-level identifications discriminated between most- and least-impacted sites, particularly in the EOH region where anthropogenic impact was greatest. Of the 543 taxa, 175 (32%) were found at ≤ 3 sites, and nearly $\frac{1}{2}$ of the taxa within a given site were occasional (found once in 3 y). Numerically rare taxa (defined as either $<1\%$ or $<0.3\%$ relative abundance within each site) accounted for 42 to 75% (WOH) and 37 to 73% (EOH) of mean site richness. Ordinations of data sets including or excluding rare taxa revealed similar impact gradients, and the % of spatial variance explained by environmental factors was similar with and without rare taxa included. Common taxa contributed noise to site-similarity patterns in the WOH region, and rare taxa provided information that was redundant with information provided by common taxa in the EOH region.

Key words: aquatic insects, sampling design, community structure, richness, relative abundance, impairment, multivariate statistics.

Rarity has been defined spatially on the basis of extent of geographic distribution, habitat specificity, and local abundance (Rabinowitz et al. 1986). Rarity has also been defined temporally, e.g., as core vs occasional taxa within a community (Magurran and Henderson 2003). Rarity can be an indicator of ecological quality/health or useful in conservation planning for freshwater systems (Cao 1999, Lenat and Resh 2001, Nijboer and Verdonschot 2004). However, different definitions of rarity can affect statistical interpretations and among-site variances in community structure. For example, Nijboer and Schmidt-Kloiber (2004) found that the “ecological quality class”

(a European multimetric index of biotic integrity) was depressed by removing species defined as spatially rare and was elevated by removing taxa with low abundances, suggesting that certain types of rarity describe different responses to environmental conditions.

All communities contain at least some rare taxa, and quantification of rare taxa may add considerable information to a data set. Preston (1948, p. 255) noted that “... it has often been a matter of comment by ecologists that one or two species are extraordinarily abundant at a particular time and place: all others seem rare in comparison”. Stream macroinvertebrate communities usually typify this statement; i.e., they are usually species-rich communities with many uncommon taxa (e.g., Morse et al. 1980, 1983, Zwick 1998, Lenat and Resh 2001), and the few extraordinarily abundant taxa influence quantification of the rare taxa.

Some researchers have recommended removal of rare taxa from data sets when evaluating biological

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health to: 1) remove outliers representing chance occurrences, 2) minimize potential taxonomic errors, 3) simplify interpretations, or 4) downweight rare taxa that might obscure among-site relationships highlighted by certain indicator taxa. Decisions for including or excluding rare taxa in a database originate in (but are not limited to) the planning stages of sampling a community because choices involving collection methods and timing are critical to the capture of rare and common taxa alike (e.g., Furse et al. 1984, Doberstein et al. 2000, Carter and Resh 2001, Cao et al. 2002, Lorenz et al. 2004). In addition, the underlying species rank-abundance relationship of a community influences the ability to capture rare taxa (e.g., richness of small samples reflects evenness among dominant taxa; Barbour and Gerritsen 1996, Courtemanch 1996).

Taxonomic resolution and rarity are intimately related, and understanding patterns of rarity requires the finest level of taxonomy. Fine taxonomic resolution adds to the degree of distinction possible among communities, particularly for stream macroinvertebrate communities where species/family ratios are high (Lenat and Resh 2001). Resh (1979) made one of the earlier calls for discrimination to species for biomonitoring purposes, stating that errors of interpretation occur when species-level enumeration is not done because species within the same genus have different responses to pollution gradients (e.g., species of the caddisfly *Ceraclea*, Resh and Unzicker 1975). Bailey et al. (2001) presented 2 perspectives regarding appropriate taxonomic resolution in benthic macroinvertebrate bioassessment studies: 1) the "lowest practicable level" (e.g., Resh 1979), which states that variations among species and genera contain valuable ecological information about various kinds of pollution exposure, vs 2) results showing minimal effects of taxonomic resolution on multivariate descriptions of variation among communities when contrasting reference (healthy) with polluted sites (e.g., Bowman and Bailey 1997). Bailey et al. (2001) further argued that both perspectives supported the view that, at a community level, family-level and higher taxonomic resolution captures most of the information related to how communities vary.

A fine level of taxonomic discrimination can contribute greatly to our ability to differentiate communities, but our primary ecological interest is in the regional (physiographic effects) and site specific (local habitat effects) factors that create a community fingerprint based on species and, perhaps, genus information. Therefore, it is critical to balance choice of taxonomic resolution with questions regarding scale and environmental hierarchy (sensu Poff 1997). Selecting coarser taxonomic levels may increase perceived

community similarity but provides a common currency for conversations among scientists and nonscientists (Bournaud et al. 1996).

Our study capitalizes on a large-scale enhanced water-quality biomonitoring project (the Project) conducted over a 3-y period at 60 sites in watersheds that contribute to the New York City (NYC) drinking-water supply (Blaine et al. 2006, Arscott et al. 2006). In Kratzer et al. (2006), analyses focused on relating macroinvertebrate communities to measured environmental variables. Our paper describes the outcome of community-level analyses designed to: 1) determine if the level of taxonomic resolution affects the statistical relationships between the macroinvertebrate assemblages and environmental variables, 2) quantify rarity using temporal, spatial, and numerical definitions, 3) determine if including rare taxa in multivariate analyses changes our perception of among-site similarity, 4) determine if the way rarity is defined (i.e., which taxa are included) changes statistical relationships with measured environmental variables, and 5) determine if the spatial variability of common taxa is correlated with the spatial variability of rare taxa.

Three statistical approaches were used. First, the effect of taxonomic resolution on the outcome of multivariate indirect gradient analyses was assessed. These ordinations were tested for correlations with measured environmental variables and interpreted in light of natural and anthropogenic gradients related to macroinvertebrate communities. Second, rare taxa were quantified based on definitions relevant to temporal, spatial, and numerical rarity. Third, indirect gradient analyses using common and rare taxa data subsets were compared and correlated with measured environmental variables to evaluate relationships between rarity, commonness, and environmental gradients.

Site description

Sixty stream sites in the NYC drinking-water-supply watersheds were visited annually in 2000, 2001, and 2002 as part of the Project (Blaine et al. 2006). Sites were evenly distributed in 2 primary regions: 1) west of Hudson River (WOH) in the upper reaches of the Delaware River and in the Catskills region (streams draining to the Hudson), and 2) east of Hudson River (EOH) in streams flowing to the Hudson River (figs 1 and 2 in Arscott et al. 2006). Arscott et al. (2006) and Dow et al. (2006) described site conditions, land use/cover (hereafter land use), and water chemistry at these 60 sites. Kratzer et al. (2006) described environmental gradients important for aquatic macroinvertebrate communities.

Methods

Macroinvertebrate sampling

Benthic macroinvertebrates were sampled annually in spring at each of the 60 sites. A Surber sampler (0.093 m²; 250- μ m-mesh net) was used to collect 16 random samples from riffle habitat along a 50- or 20-m downstream-upstream transect (depending on stream size). The 16 samples were combined in 4 large buckets (4 Surbers in each bucket) and thoroughly mixed. The contents of each bucket was split into quarters (Kratzer et al. 2006), and $\frac{1}{4}$ of the material in each bucket was retained, fixed with 5% buffered formalin, and returned to the laboratory for sorting, enumeration, and identification. In a given year, 4 composite samples were processed from each site. The mean (± 1 SD) number of individuals enumerated per sample was 216 ± 49.9 . This number amounted to, on average, >800 individuals enumerated at each site in a given year (per sample range = 102–1112 individuals). Aquatic insects, including Chironomidae, generally were identified to genus or species; other macroinvertebrates (i.e., crustaceans, mollusks, mites, flatworms, oligochaetes, and nematodes) generally were identified to a higher taxonomic level (e.g., order or family).

Data analyses

Kratzer et al. (2006) found clear differences in measures of community composition, density, and richness between regions. Therefore, taxonomic resolution and rarity patterns in each of the regions were analyzed separately and compared.

Taxonomic resolution.—The similarity of species-, genus-, family-, and order-level community composition among sites was assessed using nonmetric multidimensional scaling (NMDS) of Bray–Curtis (B–C) distance matrices. All NMDS analyses were done using the software PC-ORD (version 4.33, MjM Software Design, Gleneden Beach, Oregon). Individuals identified to coarser taxonomic levels (i.e., genus, family, or order) were carried through to the species/genus/family-level summaries. Taxa present at <5 sites within a region were removed from the species-level data matrix before summarizing coarser taxonomic levels (this practice resulted in species-level matrices that were identical to those used in Kratzer et al. 2006). EOH sites were analyzed separately from WOH sites, resulting in 8 B–C matrices and NMDS ordinations. Mean densities (3-y means) were $\log_{10}(x + 1)$ transformed prior to analysis. Ordinations were compared using the Kruskal Stress parameter that quantifies the success with which the final NMDS

iteration represents the original similarity data matrix, the number of iterations necessary to find the final solution, and the variance loadings on axes.

For each ordination, correlation coefficients (Pearson's r) were calculated for 149 environmental variables contained in a secondary matrix. Environmental variables included 76 landuse variables (Arscott et al. 2006, Kratzer et al. 2006), 30 water-chemistry variables (including ions, nutrients, organic matter, and seston; Dow et al. 2006, Kaplan et al. 2006), and 36 molecular tracer analytes and ratios (Aufdenkampe et al. 2006). Landuse variables (percentages) were arcsine-square root(x) transformed to minimize bimodality, and variables reported as concentrations were $\log_{10}(x)$ transformed prior to analysis. Water-chemistry data were mean site values from 3 summer baseflow collections (2000–2002). The degree to which primary macroinvertebrate gradients were related to environmental variables was evaluated based on the maximum r and the number of correlations where $|r| > 0.60$. Only the strongest gradients and most important descriptors of the major gradients observed for species-level ordinations are reported.

A K-means cluster analysis of the site scores from each species-level EOH and WOH NMDS solution was used to assess changes in site similarity (i.e., spatial variance) expressed in each NMDS solution as the analysis proceeded from species to order level. The K-means clustering (PAST, version 1.34; Hammer et al. 2001) was set to define 4 clusters from each set of NMDS sites scores (2-dimensional solutions for WOH analyses and 3-dimensional solutions for EOH analyses). The cluster level was set to 4 based on observations from previous ordination analyses that identified 2 primary gradients within each region (Kratzer et al. 2006). From these observations, species-level ordination axis scores were expected to define groups of sites that would be associated with the ends and middle of each gradient. Ordination is not designed to define groups/clusters, but our use of K-means clustering of NMDS site scores was solely for the purpose of assessing relative change in NMDS solutions as taxonomic (and rarity [see below]) information changed.

Significance of groups resulting from NMDS solutions was assessed using 1-way analysis of similarities (ANOSIM; Clark and Green 1988), a nonparametric test of significance between ≥ 2 groups based on a distance measure (B–C). ANOSIM tests were done using PAST software. Monte Carlo permutation was used to assess significant differences among groups (5000 permutations, Bonferroni-adjusted significance judged at $p < 0.005$). Six pairwise combinations within a region (i.e., group 1 vs 2, 1 vs 3, 1 vs 4, etc.) and 1

global model (all groups) were tested. ANOSIM was repeated for each taxonomic level within each region. Judging the statistical significance of groups identified by ANOSIM is appropriate only if the groups are chosen before the B–C distances of the species data are calculated. Therefore, using an ANOSIM to verify the statistical significance of the pattern of grouping displayed by a NMDS plot is inappropriate because both the ANOSIM and the NMDS rely on the same matrix of B–C distances. However, the *R*-values resulting from each ANOSIM computed from the various data sets are useful comparative measures of degrees of difference between groups, and other investigators provide precedence for this comparison (e.g., Defeo and Lercari 2004). The *p*-values for each comparison are reported along with each *R*-value.

Mantel tests (PC-ORD), permuted 1000 times, were used to evaluate relationships among order, family, and genus similarity matrices and species similarity matrices. The Mantel test is used to estimate the association between 2 independent similarity matrices describing the same set of entities and to test whether the associations are stronger than one would expect from chance (Sokal and Rohlf 1995).

Defining rare and common taxa.—Rare taxa were quantified based on temporal intermittency, spatial extent, and abundance. Temporally intermittent taxa (occasional taxa) were quantified by site and were defined as those taxa that were present in only 1 of 3 y. Taxa present at a site in 2 or 3 y were defined as core (Magurran and Henderson 2003). Percent core taxa and % occasional taxa were compared across sites and regions.

The spatial extent of each taxon was quantified by summing the number of taxa occurring at 1, 2, 3, . . . , 30 sites. Each year was treated as a replicate, and the 3-y mean (± 1 SD) spatial extents of each taxon were plotted as a cumulative histogram curve to summarize the % of taxa distributed (y-axis) at *x* sites (x-axis) in each region.

Numerical rarity was summarized based on 3-y mean densities (ind./m²) transformed to relative abundances (RA) for each taxon. Common and rare taxa were enumerated at each site using 3 filter levels: 1) common taxa >1% RA and rare taxa <1% RA, 2) common taxa >0.5% RA and rare taxa <0.5% RA, and 3) common taxa >0.3% RA and rare taxa <0.3% RA. Average site richness of common and rare taxa within each region was compared across numerical rarity categories (all taxa, 1%, 0.5%, and 0.3%).

Influence of rare vs common taxa on community analysis.—Two separate statistical approaches were used to examine influences of rare- and common-taxa definitions on community analyses. First, B–C similar-

ity matrices were calculated iteratively as numerically rare taxa were removed from either the WOH or EOH macroinvertebrate data sets. Iterations occurred for no taxa removed, taxa <0.05% RA removed, and (successively) taxa <0.1%, 0.3%, 0.5%, 1%, 2%, and 4% RA removed. Removal was site-specific (i.e., each site was evaluated independently) and was based on 3-y mean densities transformed to RA. Site-specific removal was aimed at simulating the outcome of decisions made in the collection phase of macroinvertebrate sampling (i.e., identifying 2000, 1000, 333, 200, 100, 50, and 25 individuals per site). Site-specific identifications averaged 2628 ind. in the 3-y mean data set. All B–C computations were done using $\log_{10}[\text{ind.}/\text{m}^2 + 1]$ transformed densities. B–C similarity matrices also were calculated iteratively as numerically common taxa were removed. Iterations occurred for none removed, taxa >4% RA removed, and (successively) taxa >2%, 1%, 0.5%, 0.3%, and 0.1% of RA removed.

B–C similarity matrices also were calculated iteratively as spatially rare taxa were removed. Iterations occurred for none removed, taxa found at only 1 of 30 sites removed, 2 of 30 sites removed, and (successively) taxa found at 3, 4, 5, 6, 7, 8, 9, 10, 15, and 20 of 30 sites removed. Last, B–C matrices were calculated iteratively as spatially common taxa were removed. Iterations occurred for taxa found at all 30 sites removed, taxa found at 29 of 30 sites removed, and (successively) taxa found at 28, 26, 21, 18, and 11 of 30 sites removed. Our goal was to quantify how the properties of the matrices changed along these removal gradients rather than to determine if these matrices were significantly different from each other (i.e., multiple Mantel tests). Therefore, mean, minimum, and maximum matrix values and taxon richness for each matrix (i.e., number of taxa remaining in the matrix) were calculated and compared within and between regions.

The 2nd statistical approach used to explore the influence of rare and common taxa on community analyses was nearly identical to analyses used to explore the effects of taxonomic resolution. NMDS was done iteratively on 5 different data subsets within each region based on differing degrees of rarity. The 5 data subsets were: 1) all taxa, 2) numerically common taxa at >0.3% RA within each site (from 3-y mean densities), 3) numerically common taxa at >1.0% RA, 4) numerically rare taxa at <1.0% of RA, and 5) numerically rare taxa at <0.3% RA. All NMDS solutions were derived in a manner identical to that described in *Taxonomic resolution* using PC-ORD. All variables included in the environmental data matrix (149 variables) were correlated with NMDS axes. Mantel tests were done for each NMDS pairwise

TABLE 1. Percent of total specimens identified to the family-, genus-, and species-level of taxonomic resolution (%) and the number (*N*) of families, genera, and species identified in each broad taxonomic group.

Taxonomic group	Total specimens	Family		Genus		Species	
		(%)	<i>N</i>	(%)	<i>N</i>	(%)	<i>N</i>
Ephemeroptera	47,452	98	10	73	27	44	43
Plecoptera	19,356	71	10	34	18	7	19
Trichoptera	15,618	94	15	79	34	29	55
Diptera (nonchironomid)	13,772	100	13	85	25	15	18
Chironomidae	68,812	100	NA	100	75	60	117
Other insects	10,976	100	15	93	24	39	17
Noninsects	31,194	23	9	0.3	4	0	2
Total specimens	207,180	85	97	70	207	36	271

comparison (15 comparisons) and Mantel's *r* was used to describe the strength of the relationship between pairs. Site groups within each NMDS were tested for similarity/differences in the NMDS 2- or 3-dimensional ordination using ANOSIM. Site groups were identical to those determined for the *Taxonomic resolution* analyses (derived using K-means clustering).

Results

Taxonomic success

At the lowest taxonomic level (species), 543 taxonomic units were identified. These units included several genus, family, and order designations for unidentified individuals (too small, damaged, or poorly known to identify to species, or noninsect taxa such as nematodes and oligochaetes). Overall, 36% of the 207,000 individuals identified were classified to the

species level, and 60% of Chironomidae were identified to species or morphotype (Table 1).

Taxonomic resolution and multivariate response

Among-site relationships detected from the species-level NMDS ordinations of both WOH and EOH sites changed and groups identified using the K-means cluster technique became less distinct as taxonomic resolution collapsed to coarser levels (Table 2, Fig. 1A–H). NMDS solutions for the 4 taxonomic levels (order, family, genus, and species) were 3-dimensional for WOH sites and 2-dimensional for EOH sites, an outcome dictated by the PC-ORD NMDS-solving algorithm. For WOH solutions, scores from all 3 dimensions were retained for analysis, but only the 2 dimensions (axes) with the highest loadings were graphed (Fig. 1A–D). All solutions were significant ($p < 0.02$) based on Monte Carlo randomization tests (50

TABLE 2. Results from NMDS ordinations for west of Hudson River (WOH) and east of Hudson River (EOH) macroinvertebrate communities summarized at species, genus, family, and order levels. Total variance explained was determined from coefficients of determination for the correlations between NMDS ordination distances and Bray–Curtis distances in the original *n*-dimensional space. Var. 1 and Var. 2 are the variances explained on the 2 axes with the highest variance loadings. Results of correlations between NMDS axes and 149 environmental variables also are presented (see text for details). Standardized Mantel's statistic (*r*) for tests of no relationship (H_0) between species similarity matrices and each subsequent taxonomic resolution were all significant (at $p < 0.002$).

Taxonomic level	Number of taxonomic units	Stress	Iterations required to obtain solution	Total variance explained	Total variance explained		Maximum environmental correlation (<i>r</i>)	No. of correlations where $r > 0.6 $	Mantel <i>r</i>
					Var. 1	Var. 2			
WOH									
Species	261	10.5	68	0.897	0.46	0.10	0.93	55	
Genus	153	11.1	73	0.883	0.33	0.29	–0.83	44	0.92
Family	55	13.8	90	0.804	0.39	0.25	0.83	41	0.67
Order	16	14.2	216	0.823	0.46	0.20	–0.71	7	0.30
EOH									
Species	224	13.6	56	0.893	0.68	0.21	0.79	35	
Genus	156	12.0	89	0.914	0.75	0.17	0.78	23	0.96
Family	50	11.8	88	0.924	0.69	0.24	–0.75	29	0.89
Order	20	16.5	109	0.870	0.29	0.58	0.78	25	0.79

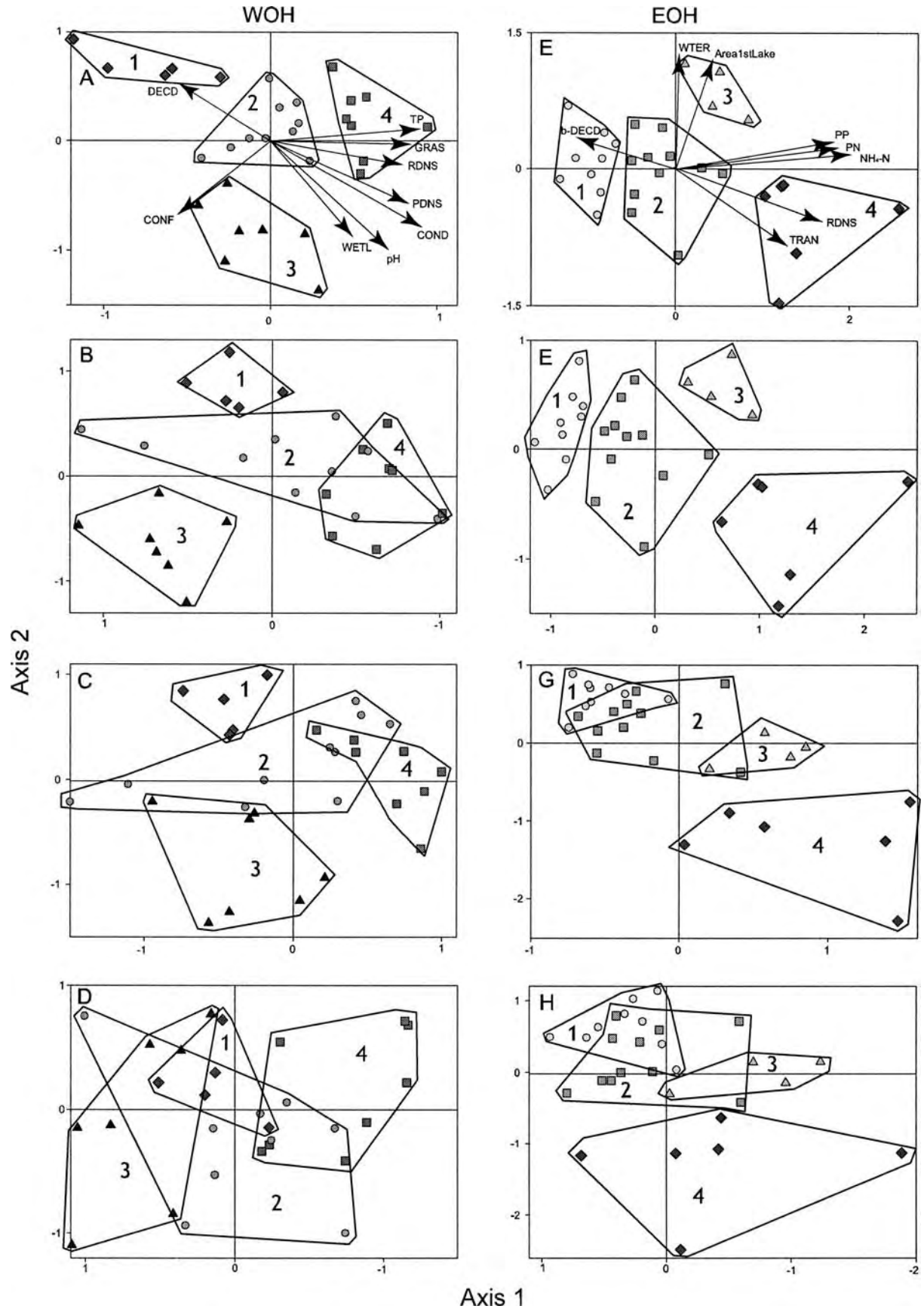


TABLE 3. *R* statistics from 1-way analysis of similarity of Bray–Curtis distances (based on taxon density) and pairwise comparisons between groups of sites (1–4) defined using K-means clustering (see Methods) within either the west of Hudson River (WOH) or east of Hudson River (EOH) regions at decreasing taxonomic resolution. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.005$, ns = $p > 0.05$.

Comparison	Species	Genus	Family	Order
WOH				
Global	0.62***	0.67***	0.58***	0.20***
1 vs 2	0.55***	0.43***	0.18 ^{ns}	0.05 ^{ns}
1 vs 3	0.90***	0.91***	0.78***	0.03 ^{ns}
1 vs 4	0.96***	0.91***	0.71***	0.28*
2 vs 3	0.46***	0.46***	0.34***	0.21*
2 vs 4	0.27***	0.21**	0.16*	0.19*
3 vs 4	0.90***	0.94***	0.85***	0.56*
EOH				
Global	0.65***	0.63***	0.61***	0.47***
1 vs 2	0.31***	0.29***	0.19***	0.09 ^{ns}
1 vs 3	0.98***	0.98***	0.62***	0.87***
1 vs 4	1.00***	0.99***	0.99***	0.82***
2 vs 3	0.70***	0.69***	0.83***	0.56***
2 vs 4	0.71***	0.74***	0.98***	0.59***
3 vs 4	0.76***	0.53**	0.41*	0.19 ^{ns}

permutations) comparing Kruskal Stress values in randomized vs computed solutions. All Kruskal Stress values were < 17.0 . The lowest Kruskal Stress value for the EOH ordinations (Fig. 1E–H) and the highest variance explained (derived from the coefficient of determination for the correlation between NMDS ordination distances and distances in the original n -dimensional B–C matrix space) was at the family level (Table 2; Fig. 1G). In contrast, the lowest Kruskal Stress value for the WOH ordinations and the highest variance explained was at the species level (Table 2; Fig. 1A).

For the WOH region, the highest r -value and the greatest number of environmental variables with $r > |0.6|$ were found with species-level taxonomic resolution (Table 2). These correlation statistics consistently declined as taxonomic resolution collapsed to coarser levels. For the EOH region, the maximum r -values were similar for all taxonomic resolution levels ($|r| = 0.75$ – 0.79), but r was greatest at the species level.

ANOSIM R -values indicated that groups became less distinct (R decreased) as taxonomic resolution

collapsed to coarser levels in both regions (Table 3). For the WOH region, the pattern of decreasing R as taxonomic resolution collapsed to coarser levels was consistent for all comparisons except group 2 vs 4 at the order level (Table 3). Thus, ANOSIM results, NMDS output, and Mantel correlations indicated a change in community information that consistently resulted in fewer taxa–environment correlations and poorer among-site/group discriminatory power as taxonomic resolution collapsed to coarser levels. For the EOH region, R generally decreased as taxonomic resolution collapsed to coarser levels, but several group comparisons (i.e., 1 vs 3, 2 vs 3, and 2 vs 4) had peak R values at family- or order-level taxonomic resolution (Table 3). Thus, ANOSIM results, NMDS output, and Mantel correlations described a change in community information with changing taxonomic resolution; however, that change did not result in lower correlations with environmental variables and statistical ability to discriminate among sites/groups was maintained at coarser levels of taxonomic resolution.

Definition of rare and common taxa

Temporally rare taxa (present in 1 of 3 y within a site) accounted for nearly 50% of taxon richness at a site, regardless of region. Temporal rarity did not appear to differ between WOH and EOH regions. Nearly 50% of taxa in the WOH region were found at ≤ 5 sites (Fig. 2A), and $> 50\%$ of taxa (species-level) in the EOH region were found at ≤ 4 sites (depending on year; Fig. 2B).

Mean site richness varied slightly by year and ranged from 56 to 127 for WOH sites and 18 to 111 for EOH sites. At WOH sites, taxa that were numerically rare at $< 0.3\%$ RA within a site accounted for $\sim 42\%$ of mean richness at a site, whereas taxa that were numerically rare at $< 1.0\%$ RA within a site accounted for $\sim 75\%$ of mean richness at a site (Fig. 3A). At EOH sites, taxa that were numerically rare at $< 0.3\%$ RA within a site accounted for $\sim 37\%$ of mean richness at a site, whereas taxa that were numerically rare at $< 1.0\%$ RA within a site accounted for $\sim 71\%$ of mean richness at a site (Fig. 3B). Numerical rarity (taxa at $< 0.3\%$ RA) was positively correlated with total site richness (WOH: $r = 0.86$, EOH: $r = 0.94$) but was poorly

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FIG. 1. Nonmetric Multidimensional Scaling (NMDS) plots based on Bray–Curtis distance matrices of macroinvertebrate densities at sites west of Hudson River (WOH) and east of Hudson River (EOH) summarized at the species (A, E, respectively), genus (B, F), family (C, G), and order (D, H) levels. Lines are drawn around groups of sites identified using K-means cluster analysis (k set to 4 groups) of species-level NMDS axes scores (see Methods). Symbols follow K-means groups. Environmental vectors in panels (A) and (E) are for environmental variables with the highest correlation coefficients for either axis (see Arscott et al. 2006 for variable names and abbreviations).

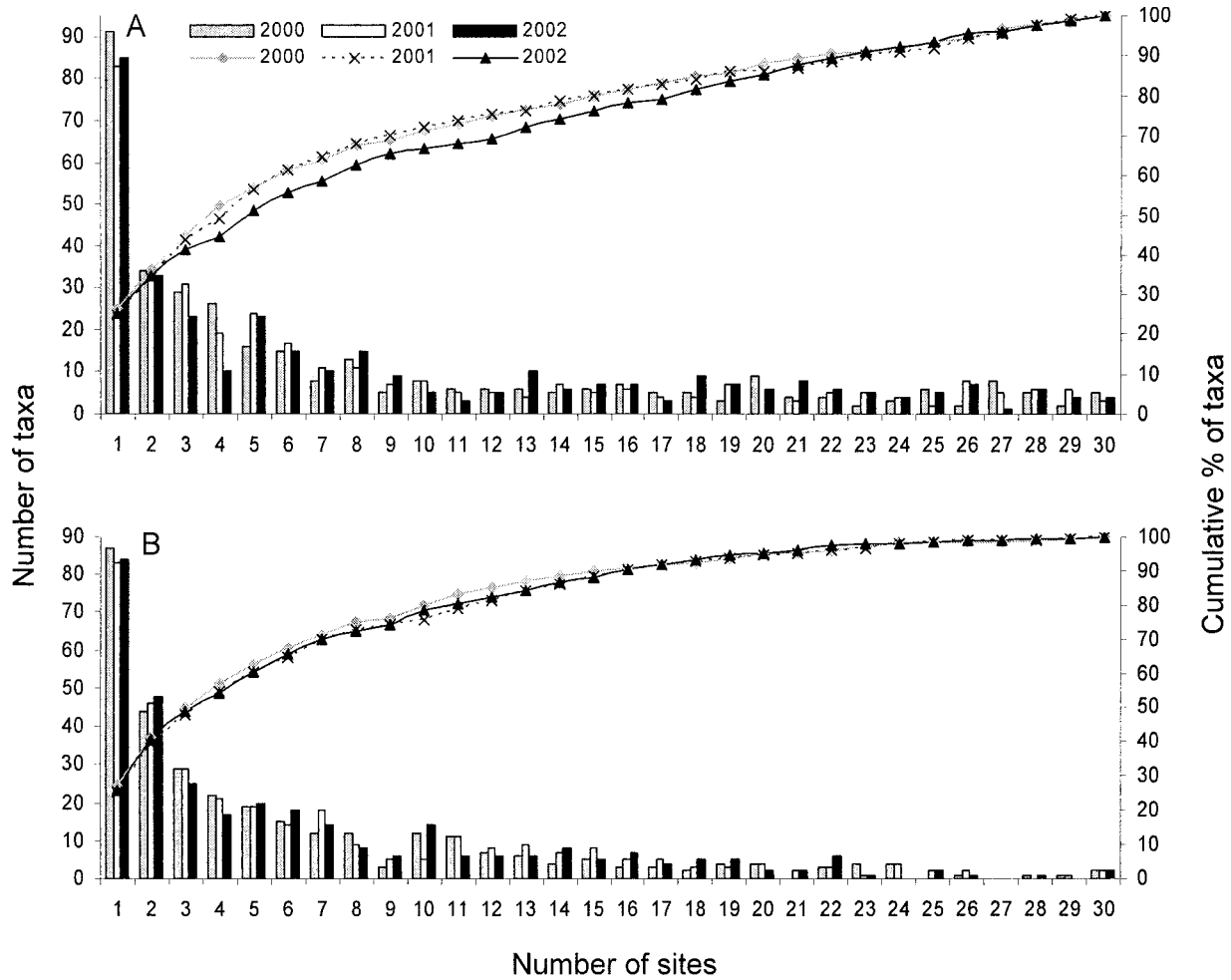


FIG. 2. Spatial extent of taxonomic units (species-level data set; see Methods) in the west of Hudson River (WOH: A) and east of Hudson River (EOH: B) regions. Bars quantify the number of taxonomic units that were found at 1 site, 2 sites, 3 sites, . . . , and 30 sites based on 1 spring sampling event per year in 2000, 2001, and 2002. The lines quantify the cumulative number of taxonomic units that were distributed at 1, ≤ 2 , ≤ 3 sites, . . . , and ≤ 30 sites.

correlated with total site density (WOH: $r = 0.26$, EOH: $r = 0.52$).

In both regions, taxa with broad spatial distributions typically were abundant and had high maximum and mean densities (Fig. 4A, B). No taxon in either region could be described as being both low-density and ubiquitous when low density was defined based on the 50th percentile RA criteria. In both regions, the mean densities of widely distributed taxa (present at ≥ 20 sites) were ranked $\geq 57^{\text{th}}$ percentile (WOH: 267 of 464 taxa, EOH: 263 of 436 taxa) at any site. Most taxa with spatially restricted distributions (present at ≤ 4 sites) had low densities (Fig. 4A, B).

Site similarity and the removal of rare and common taxa

As numerically common or rare taxa were removed from both WOH and EOH data matrices, the mean B-

C similarity among sites declined (Fig. 5A, B, E, F). The effect of reducing mean similarity by removing rare taxa was surprising. This result was driven by the removal of numerically common or rare taxa based on relative abundance *within* each site. This removal simulated choices made during the sampling and enumeration phases of methods and not choices made post hoc to remove all taxa with mean abundance across sites that was below some criterion (e.g., 1%). The range of matrix similarities remained constant as numerically common taxa were removed from both WOH and EOH regions (Fig. 5A, B), suggesting little change in the relative structure within each B-C matrix. In contrast, the range of matrix similarities increased as numerically rare taxa were removed (Fig. 5E, F) because a few sites became more similar after removals, particularly for WOH comparisons.

Criteria for removal of spatially common or rare

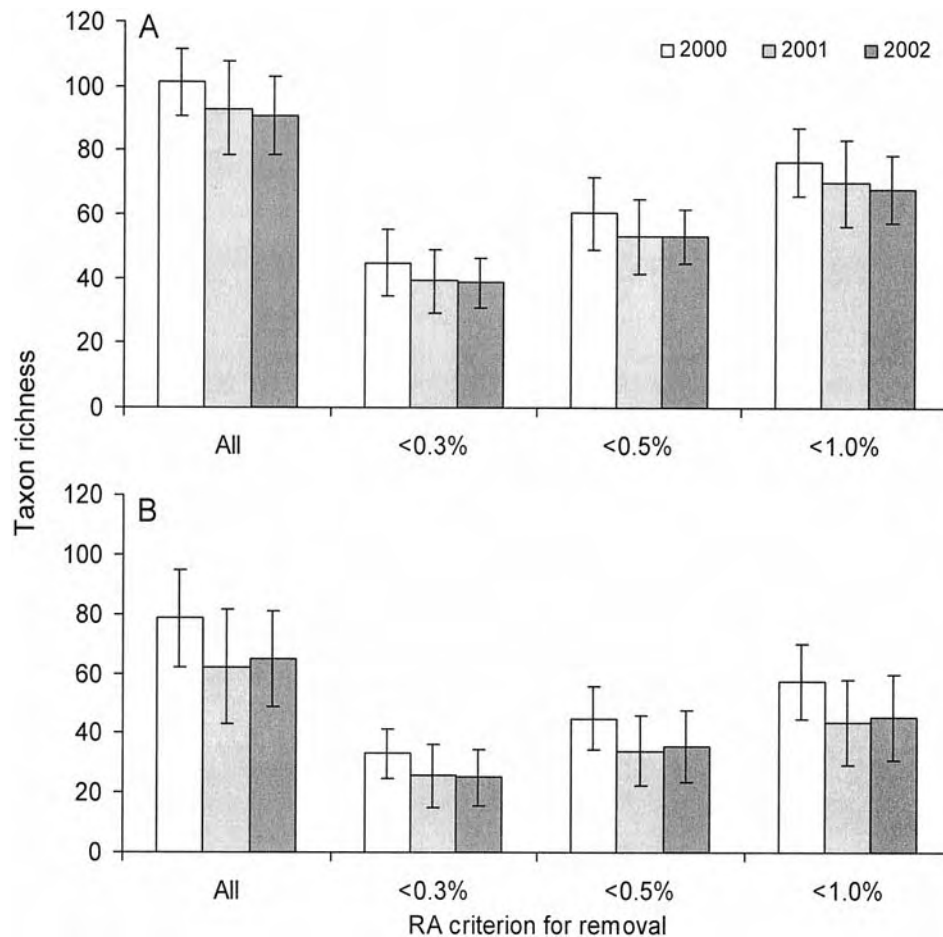


FIG. 3. Mean (± 1 SD) site taxon richness (species level) by year ($n = 30$ sites) in the west of Hudson River (WOH: A) and east of Hudson River (EOH: B) regions for data subsets consisting of all taxa, or from which rare taxa $<0.3\%$ relative abundance (RA), rare taxa $<0.5\%$ RA, and rare taxa $<1.0\%$ RA were removed.

taxa were based on the distribution of each taxon across sites in each region. As spatially common taxa were removed from both WOH and EOH data matrices, mean similarity among sites declined (Fig. 5C, D). Removal of spatially rare taxa (Fig. 5G, H) caused mean, minimum, and maximum matrix values to increase (albeit only slightly at first) for both regions. These patterns illustrated that spatial differences in rare taxa were important components helping to define community differences among sites.

Simulated lower sampling intensity or effort resulted in greater community dissimilarity, and similarity declined as either numerically or spatially common taxa were removed. As expected, removal of spatially rare taxa caused similarity to increase, but removal of numerically rare taxa caused mean similarity to decrease because taxa were differentially removed from sites where they were numerically rare and remained at sites where they were more common.

Rare and common taxa in multivariate space and relationships with environmental variables

NMDS ordination was applied to 5 data subsets derived using abundance-based definitions of common and rare taxa to investigate whether lower sampling intensity would affect interpretations of among-site similarity in macroinvertebrate communities or macroinvertebrate–environment relationships. The total number of taxonomic units and mean site richness and density for each data subset are reported in Table 4.

NMDS solutions for WOH data subsets were 3-dimensional, and all dimensions were used to compute summary statistics; however, graphs of the solutions project only the 2 axes with the greatest variance loadings (Fig. 6A–E). NMDS solutions for EOH data subsets were either 2- or 3-dimensional depending on the data subset (Fig. 6F–J). For both regions, NMDS solutions based on all taxa had the

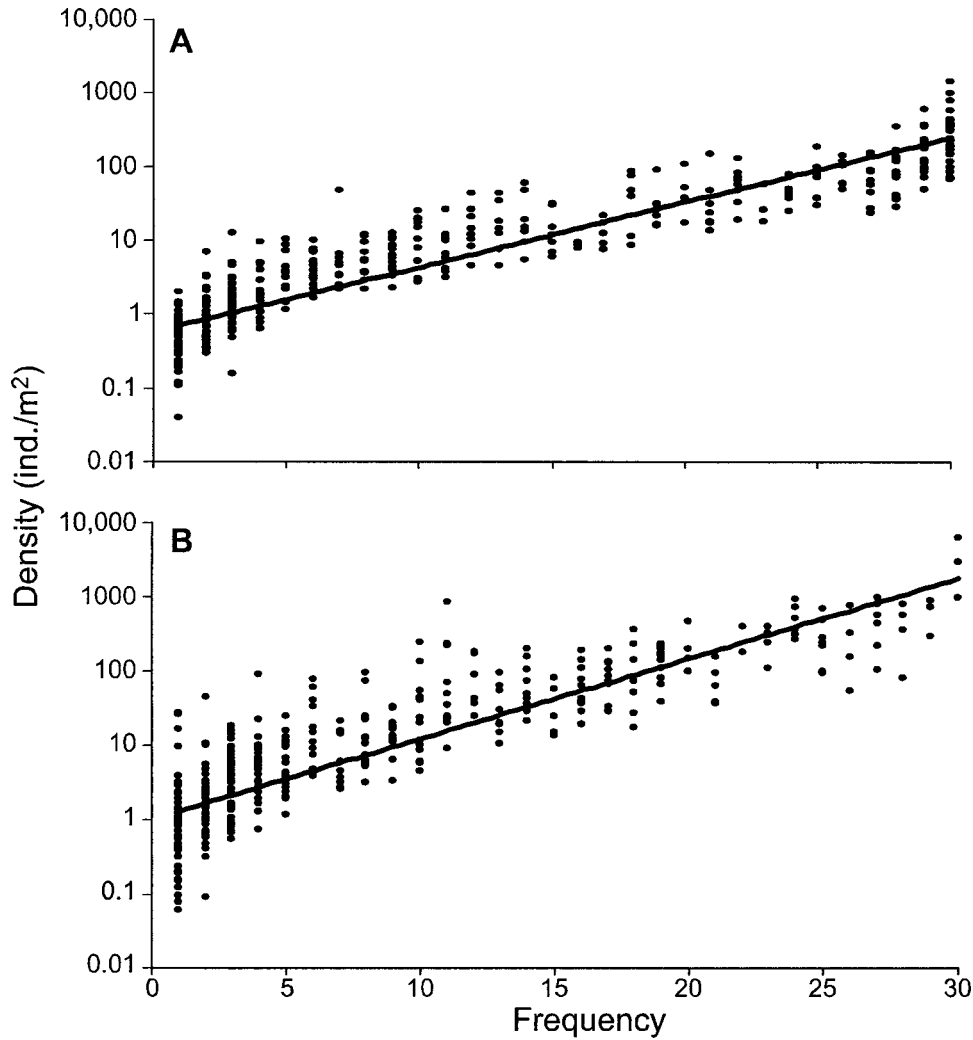


FIG. 4. Mean macroinvertebrate density ($n=3$ y) for each taxon (species level) in 30 sites west of Hudson River (WOH: A) and 30 sites east of Hudson River (EOH: B) regions vs the number of sites from which the taxon was collected (frequency). Four hundred sixty-four taxa were collected from the WOH region and 436 taxa were collected in the EOH region. The solid line is an exponential regression line with $r^2 = 0.85$ and $r^2 = 0.76$ for the WOH and EOH regions, respectively.

lowest Kruskal Stress, greatest total variance explained, and greatest variance loading on the 1st axis (Table 5). For both regions, NMDS solutions based on the most conservative definition of rare taxa (<0.3% RA within a site) had the highest Kruskal Stress, lowest total variance explained, and lowest variance loading on the 1st axis. However, for the WOH region, NMDS solutions based on rare taxa <0.3% RA were better correlated with environmental variables than NMDS

solutions based on common taxa >1.0% RA. In contrast, for the EOH region, all NMDS solutions had similar maximum correlations with environmental variables, but the NMDS solution based on rare taxa <0.3% RA had the fewest correlations with environmental variables where $r > |0.6|$.

In both regions, the all taxa data subset was best correlated (Mantel r) with the rare taxa <1% RA data subset and was more poorly correlated with the

FIG. 5. Mean (triangles and solid line) Bray–Curtis (B–C) similarities (\pm range [dashed lines]; and total [gray bars]) number of taxa in matrices from west of Hudson River (WOH: A, C, E, G) and east of Hudson River (EOH: B, D, F, W) data subsets from which numerically common (A, B), spatially common (C, D), numerically rare (E, F), and spatially rare (G, H) taxa were removed. See Methods for details of removal methods. RA = relative abundance, Frequency = number of sites within a region at which a taxon was collected.

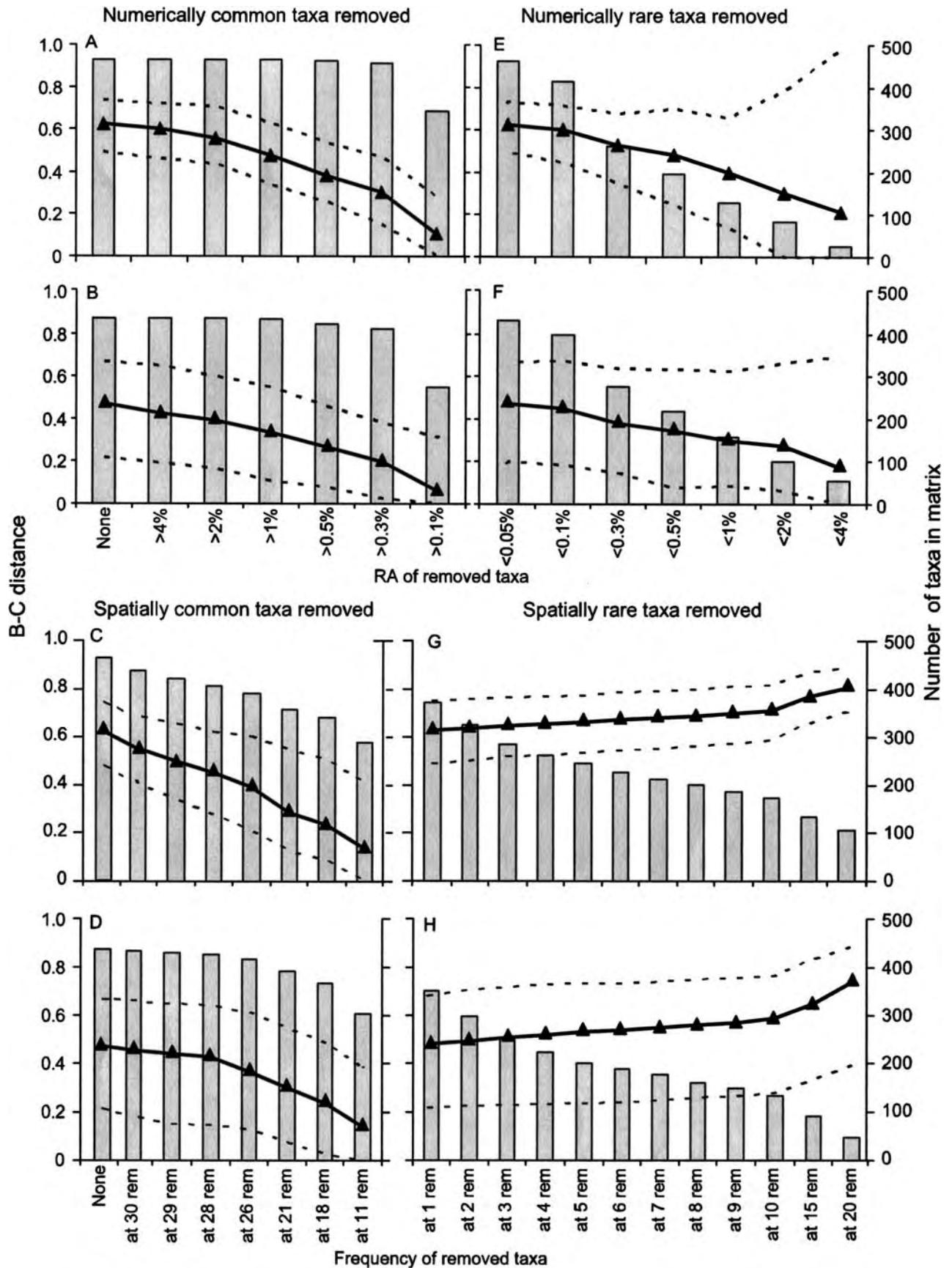


TABLE 4. Mean ($n = 3$ y) taxon richness and macroinvertebrate densities for west of Hudson River (WOH) and east of Hudson River (EOH) data subsets ($n = 30$ sites in each data subset) summarizing all taxa, common taxa $>0.3\%$ relative abundance (RA), common taxa $>1\%$ RA, rare taxa $<1\%$ RA, and rare taxa $<0.3\%$ RA (see Methods).

Data subset	Total taxonomic units	Taxon richness		Density (ind./m ²)	
		Mean	Range	Mean	Range
WOH					
All taxa	464	163.6	131–196	27,730	9518–53,257
Common $>0.3\%$ RA	131	64.3	51–76	22,947	7869–44,286
Rare $<1\%$ RA	370	134.7	106–167	10,506	4022–21,789
Common $>1\%$ RA	56	21.2	12–29	14,633	4924–27,839
Rare $<0.3\%$ RA	356	88.5	71–118	3533	1286–6,894
EOH					
All taxa	436	120.3	49–172	50,464	13,256–215,701
Common $>0.3\%$ RA	116	46.2	20–66	42,962	11,069–199,223
Rare $<1\%$ RA	345	94.8	36–144	11,808	3570–26,784
Common $>1\%$ RA	41	14.8	7–23	26,632	6918–133,539
Rare $<0.3\%$ RA	309	60.3	26–94	3905	1271–8843

common taxa $<1\%$ RA data subset (Table 6). In addition, pairwise comparisons between the common taxa $>1\%$ RA data subset and other data subsets had consistently low Mantel r -values. The poorest correlation was between the common taxa $>1\%$ RA and the rare taxa $<0.3\%$ RA data subsets (Table 6).

NMDS solutions (Fig. 6A–J) based on the common taxa $>1\%$ RA data subset (Fig. 6D, I) did not maintain the site-similarity patterns (i.e., groups identified by K-means cluster analysis were not maintained) that were evident in many of the other iterations in our analyses, particularly for the WOH sites (Fig. 6D). ANOSIM R -values were lowest for comparisons among WOH groups identified from NMDS solutions based on the common taxa $>1\%$ RA data subset (Table 7, Fig. 6D). In contrast, ANOSIM R -values were lowest for comparisons among EOH groups identified from NMDS solutions based on the rare taxa $<0.3\%$ RA data subset (Table 7, Fig. 6J).

Our primary interpretations from these analyses were related to region-specific environmental degradation, the importance of taxa between 0.3 and 1% RA, and the degree to which rare taxa contributed noise in data subsets. Environmental gradients in the EOH region were strong (several highly degraded streams) and correlated well with all data subsets tested. Environmental gradients in the WOH region were less strong than in the EOH region. The environmental gradient in the WOH region correlated well with all data subsets except common taxa $>1\%$ RA. Thus, meaningful community–environmental differences among WOH sites could not be discriminated using common taxa $>1\%$ RA. Taxa with RA between 0.3 and 1% appeared to influence strongly the outcomes of analyses that included them. Data subsets based on

rare taxa (defined at both $<1\%$ RA and $<0.3\%$ RA levels) were correlated with the same environmental gradients revealed using all taxa (i.e., they did not express novel relationships). Moreover, excluding rare taxa did not alter among-site similarities identified in ordinations based on all taxa (Fig. 6A, F) at species-level taxonomic resolution (Fig. 1A, E), suggesting that rare taxa did not add noise to data sets.

Discussion

Sampling and taxonomic effort for the Project was rigorous and resulted in mean species richness values of nearly 59 taxa per EOH site and 82 taxa per WOH site in any given year (conservative estimates excluding unrecognized specimens, e.g., small stoneflies). Maximum 3-y total richness at one WOH site approached 195 taxa. However, this effort was far from exhaustive from the perspective of making a complete inventory of taxa. For example, inventories of aquatic insect species yielded lists of >700 collected from the Breitenbach in Germany (Zwick 1998), >650 collected from the Upper Three Runs Creek in South Carolina (J. C. Morse, Clemson University, personal communication), >300 collected from White Clay Creek (B. W. Sweeney, Stroud Water Research Center, personal communication), and between 153 and 230 at selected sites in North Carolina (Lenat and Resh 2001). Nevertheless, our sampling and taxonomic effort was at least commensurate with other bioassessment efforts world wide (e.g., Diamond et al. 1996, Zamora-Muñoz and Alba-Tercedor 1996, Houston et al. 2002, Bailey et al. 2004, Nijboer and Schmidt-Kloiber 2004).

Does taxonomic resolution affect statistical relationships between macroinvertebrate communities and environmental variables?

In our study, species identifications provided the greatest among-site discrimination and the most robust relationships with environmental variables for both regions. However, family- and genus-level identifications of EOH communities and genus-level identifications of WOH communities were strongly correlated with species-level B–C similarity matrices, indicating that patterns of among-site differences generally were maintained at coarser taxonomic levels. Furse et al. (1984) observed that species data provided a more reliable site categorization than family data, and they showed that species data carried higher information content than family data, resulting in higher β diversity when species data were used. King and Richardson (2002) found that community–environment relationships identified using family-level data were inferior to relationships identified using genus- and species-level data, primarily because chironomids made up a large proportion (20%) of total species in the community. In our data set, chironomids also made up a large proportion of total species (~35%), and the large number of insect taxa per order (mean = 56, range = 2–200) undoubtedly contributed to community–environment relationships that were more robust when based on species-level identifications than when based on family-level identifications, particularly when the environmental gradient was subtle, as in the WOH region.

On the other hand, Bournaud et al. (1996), Hewlett (2000), Feminella (2000), and Hawkins and Vinson (2000) each suggested that broad-scale patterns could be discriminated equally well by species-, genus-, or family-level identifications, although Bournaud et al. (1996) found that species-level identifications did reveal slightly more longitudinal change along a European river than family-level identifications. Bowman and Bailey (1997) found that genus-level identifications did not describe strikingly different community patterns than higher-level identifications (e.g., family or order), but they did not specify the geographic scale at which their data sets were collected. Several marine invertebrate studies (Warwick 1988, James et al. 1995, Vanderklift et al. 1996, Defeo and Lercari 2004) also suggest that coarse-level taxonomy results in minimal loss of site discrimination ability relative to discrimination possible with fine-level taxonomy. However, direct comparison between marine and freshwater studies of the effects of choosing levels of taxonomic resolution is difficult because diversity among coarse taxonomic levels (e.g.,

phylum, class, order) is greater for marine communities than for typical freshwater invertebrate communities where species per family ratios are higher (Lenat and Resh 2001). In marine studies where species per family ratios were high, species information resulted in enhanced discrimination among sites (Narayana-swamy et al. 2003, Anderson et al. 2005).

EOH sites were distributed along a very strong forest–urban gradient, whereas WOH sites were distributed along a forest–agriculture gradient, and anthropogenic impacts were stronger at urban EOH sites than at agricultural WOH sites (Arscott et al. 2006, Aufdenkampe et al. 2006, Dow et al. 2006, Kaplan et al. 2006, Kratzer et al. 2006). Moreover, community structure was influenced by upstream reservoirs at several EOH sites (Kratzer et al. 2006). The range of values in the B–C matrices for each region reflected the differences in the strengths of the environmental gradients in the 2 regions (i.e., range of similarity values in EOH \gg WOH). In the EOH ordinations, family-level identifications were adequate for separating forested, urban, and reservoir outlet sites because the gradients in the EOH region were strong. On the other hand, in the WOH ordinations, genus- or species-level identifications were necessary to differentiate among sites because the anthropogenic stressors and, therefore, the gradients were subtle. Waite et al. (2004) reported a similar result using sites sampled in the Mid-Atlantic Highlands where family- and genus-level identifications provided similar discrimination among sites along a gradient with extreme contrasts (severe-to-least disturbed) but genus-level identifications (particularly of chironomids) provided greater sensitivity to more subtle impairments.

Taxonomic choice and sampling design

Bailey et al. (2001) stated that decisions regarding taxonomic resolution must be made with careful consideration for whether fine-scale resolution would contribute significantly more information than coarse-scale taxonomic information for the description of a site. Lenat and Resh (2001) pointed to the value of genus- and species-level information for indices, such as the Hilsenhoff Biotic Index (Hilsenhoff 1988), that are based on tolerance values, particularly when species within the same genus have differential responses or tolerances (Resh and Unzicker 1975). For example, a European multimetric index was strongly affected by taxonomic resolution because certain components of that metric required species-level autecological information (Schmidt-Kloiber and Nijboer 2004). However, information related to species-specific tolerance values can be limited because of

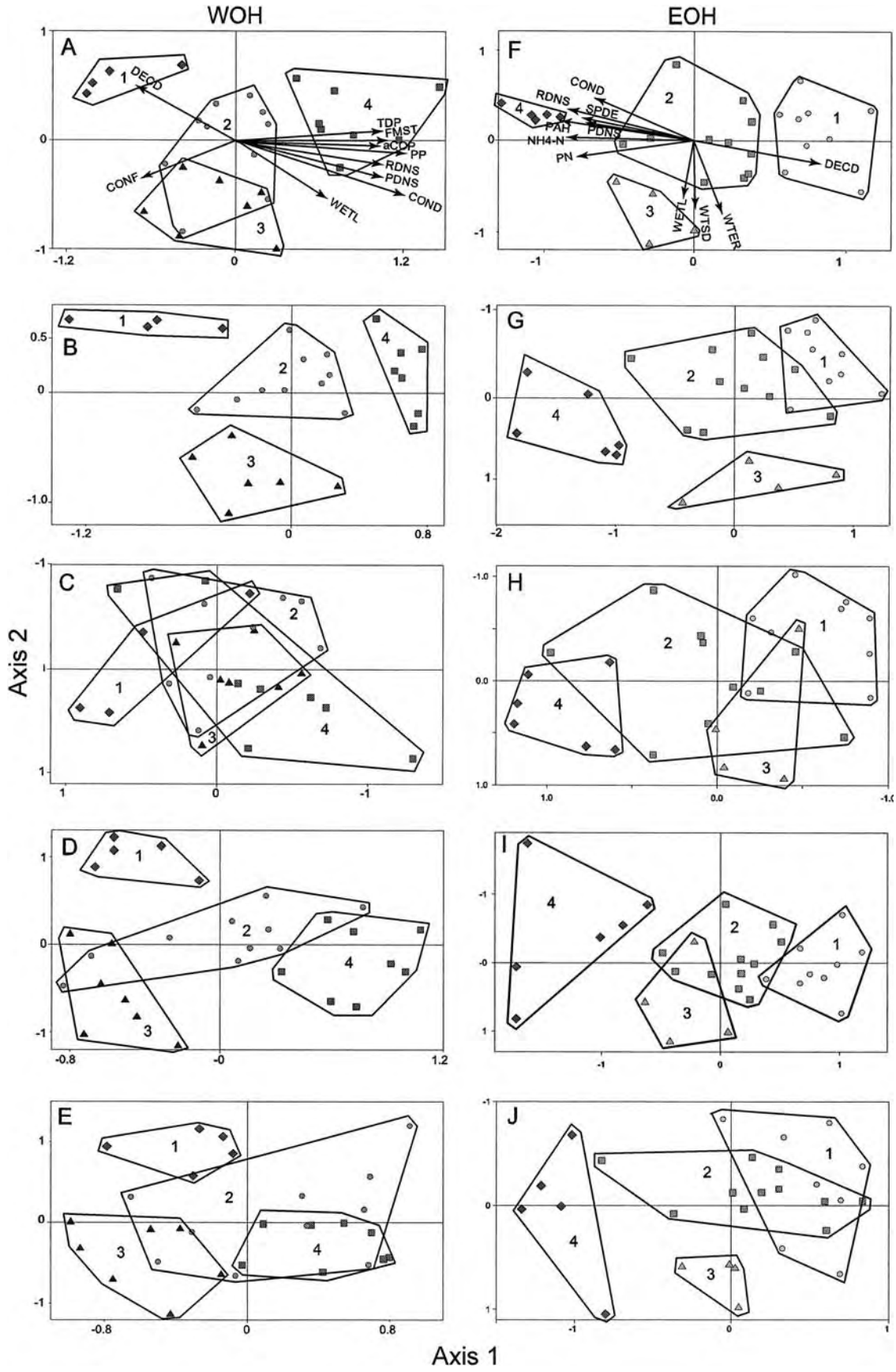


TABLE 5. Results from NMDS ordinations for west of Hudson River (WOH) and east of Hudson River (EOH) macroinvertebrate communities based on data subsets consisting of all taxa, common taxa >0.3% relative abundance (RA), common taxa >1% RA, rare taxa <1% RA, and rare taxa <0.3% RA (see Methods). Total variance explained was determined from coefficients of determination for the correlations between NMDS ordination distances and Bray–Curtis distances in the original n -dimensional space. Var. 1 and Var. 2 are the variances explained on the 2 axes with the highest variance loadings. Results of correlations between NMDS axes and 149 environmental variables also are presented (see text for details).

Data subset	Number of taxonomic units	Stress	Iterations required to obtain solution	Total variance explained	Var. 1	Var. 2	Maximum environmental correlation (r)	No. of correlations where $r > 0.6 $
WOH								
All taxa	464	10.4	69	0.91	0.41	0.29	0.90	57
Common >0.3% RA	131	15.8	122	0.76	0.34	0.23	0.91	61
Rare <1% RA	370	14.3	144	0.80	0.39	0.22	0.88	47
Common >1% RA	56	16.0	68	0.75	0.39	0.22	-0.66	5
Rare <0.3% RA	356	20.4	181	0.58	0.28	0.17	0.79	39
EOH								
All taxa	436	9.0	62	0.94	0.69	0.15	-0.78	40
Common >0.3% RA	116	15.4	85	0.85	0.60	0.25	-0.77	15
Rare <1% RA	345	17.3	83	0.80	0.50	0.30	0.78	17
Common >1% RA	41	14.5	66	0.78	0.34	0.24	0.80	20
Rare <0.3% RA	309	17.9	99	0.71	0.26	0.23	-0.70	12

the dearth of autecological studies for many taxa (with the possible exception of western Europe).

Debate over the appropriate level of taxonomic resolution has been related to: 1) the geographic scale of the study, 2) taxonomic complexity (species/family ratios), and 3) the statistical dichotomy between multimetric indices and multivariate approaches. The information expressed at various taxonomic levels varies in importance depending on these factors and the degree to which rare taxa have been included in the data set. Kratzer et al. (2006) demonstrated that broad-scale differences in communities between the WOH and EOH regions (biogeographic influences) were evident using family-level taxonomic information and presence/absence data. Furthermore, differences in communities among sites within the EOH region were easily identified using order-level taxonomic information, in part because several severely degraded sites were included in this comparison. Nevertheless, our results and those of Kratzer et al. (2006) also emphasize the importance of species- and genus-level taxonomic information for identifying differences in communities among sites within the WOH region where environmental gradients were

subtle and coarse taxonomic resolution and use of a multimetric index (see Kratzer et al. 2006) homogenized important differences among sites.

Incorporating the anticipated strength of the environmental gradient in question (e.g., severe impacted-pristine condition gradients, geographic scale) and estimating the sensitivity required to reveal community changes along that gradient (depending on the question and the environmental gradient of concern) will lead to more informed decisions regarding the required level of taxonomic resolution. However, questions often change during a study, and the strength of environmental gradients often is unknown. These realities favor planning (and budgeting) to identify taxa to the lowest taxonomic level possible. The value of developing a species-level baseline is greatest for a long-term study because reworking historic samples for species determinations is often impossible or impractical, and family-level data are of little use for questions that are best addressed with genus and species identifications. The practicality of lowest-possible-level identifications has been discussed frequently in the stream bioassessment literature, and the discussion has focused mainly on costs

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FIG. 6. Nonmetric Multidimensional Scaling (NMDS) plots based on Bray–Curtis distance matrices of data subsets for sites west of Hudson River (WOH) and east of Hudson River (EOH) consisting of all taxa (A, F), common taxa >0.3% relative abundance (RA: B, G), rare taxa <1% RA (C, H), common taxa >1% RA (D, I), and rare taxa <0.3% RA (E, J). See Methods for details. Lines are drawn around groups of sites identified using K-means cluster analysis (k set to 4 groups) of species-level NMDS axes scores (see Methods). Symbols follow K-means groups. Environmental vectors in panels (A) and (F) are for environmental variables with the highest correlation coefficients for either axis (see Arscott et al. 2006 for variable names and abbreviations).

TABLE 6. Standardized Mantel's statistic (*r*) for tests of no relationship (H_0) between Bray–Curtis distance matrices calculated for data subsets consisting of all taxa, common taxa >0.3% relative abundance (RA), common taxa >1% RA, rare taxa <1% RA, and rare taxa <0.3% RA of the macroinvertebrate community data set. Comparisons above the diagonal are for west of Hudson River data subsets; comparisons below the diagonal are for east of Hudson River data subsets.

	All taxa	Common 0.3% RA	Rare <1% RA	Common >1% RA	Rare <0.3% RA
All Taxa	–	0.76	0.89	0.64	0.72
Common >0.3% RA	0.90	–	0.63	0.62	0.59
Rare <1% RA	0.94	0.81	–	0.62	0.71
Common >1% RA	0.69	0.79	0.63	–	0.40
Rare <0.3% RA	0.75	0.68	0.80	0.50	–

related to taxonomic expertise and on the taxonomic challenges of identifying small organisms or poorly known groups (e.g., Furse et al. 1984, Jackson and Resh 1988, Barbour and Gerritsen 1996, Carter and Resh 2001). Nevertheless, in our study, identifying ~70% of our specimens to genus and 35% to species added important ecological information that went beyond the results of statistical analyses based on family- or order-level identifications.

How prevalent are rare taxa and how is prevalence related to temporal, spatial, and numerical definitions of rarity?

Cao and Larsen (2001) stated that aquatic entomologists typically refer to rare species as: 1) spatially

TABLE 7. Values of the *R* statistic from 1-way analysis of similarity of Bray–Curtis distances and pairwise comparisons between groups of sites (1–4) defined using K-means clustering (see Methods) of data subsets consisting of all taxa, common taxa >0.3% relative abundance (RA), common taxa >1% RA, rare taxa <1% RA, and rare taxa <0.3% RA for the west of Hudson River (WOH) or east of Hudson River (EOH) regions. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.005$, ns = $p > 0.05$.

	All taxa	Common >0.3% RA	Rare <1% RA	Common >1% RA	Rare <0.3%
WOH					
Global	0.60***	0.47***	0.53***	0.21***	0.41***
1 vs 2	0.53***	0.42***	0.42*	0.06 ^{ns}	0.38***
1 vs 3	0.92***	0.71***	0.89***	0.51*	0.66***
1 vs 4	0.95***	0.86***	0.93***	0.45***	0.85***
2 vs 3	0.42***	0.32***	0.34***	0.23*	0.18*
2 vs 4	0.29***	0.15 ^{ns}	0.21*	0.02 ^{ns}	0.23*
3 vs 4	0.89***	0.70***	0.84***	0.27*	0.55***
EOH					
Global	0.63***	0.63***	0.57***	0.57***	0.48***
1 vs 2	0.32***	0.24***	0.30***	0.26*	0.20*
1 vs 3	0.97***	0.94***	0.83***	0.84***	0.72***
1 vs 4	0.96 ^a	1.00***	0.89***	1.00***	0.82***
2 vs 3	0.64***	0.65***	0.64***	0.44**	0.37*
2 vs 4	0.69***	0.66***	0.65***	0.49**	0.63***
3 vs 4	0.72**	0.81**	0.49*	0.6*	0.33*

restricted in low or high numbers, or 2) exhibiting broad habitat selection and low local density. In our study, rarity was pervasive regardless of its definition. Across all 60 sites, temporally rare taxa (collected once in 3 y) ranged from 40 to 60% of total taxon richness, ~50% of taxa were distributed at ≤5 sites within a region (variable by year and region) and, on average, ~40% of taxa at a site had RA <0.3% of the site total. In a 7 to 9 y study of North Carolina streams, taxa collected in any 1 summer accounted for only ~50% of the total species collected during the whole study (Lenat and Resh 2001). In lowland streams in the Netherlands, removing rare taxa with mean RA ≤0.3% eliminated nearly 50% of taxa (from 865 taxa to 424) and removing taxa based on distribution (found at ≤4% of sites) eliminated ~1/3 of taxa (Nijboer and Schmidt-Kloiber 2004). In California, between 17 and 33% of taxa collected annually over periods of 7 to 8 or 19 to 20 y occurred in only 1 y of the collections (Resh et al. 2005).

One form of rarity (i.e., a wide distribution and low density) was not common in our data set because ubiquity and density were positively correlated. The density of widely distributed (at ≥20 sites) taxa ranked ≥57th percentile at any site where a widely distributed taxon was found. Hanski et al. (1993) concluded that no single, universal explanation for the positive distribution–abundance relationship existed. Hanski et al. (1993) further concluded that a “sampling artifact” phenomenon could explain this result, but did not reveal the key processes that generate this relationship. Gaston (1998) also observed that abundant species tended to be widely distributed, and that the number of individuals typically increased at a faster rate than did the area over which they were distributed, resulting in both high local densities and wide distributions.

The presence/absence of both rare and common taxa can be related to anthropogenic disturbance. For example, EOH sites had fewer ubiquitous taxa (taxa distributed at 27–30 sites) than WOH sites (Fig. 2), and

spatiotemporal turnover (organisms appearing at different sites in different years) accounted for a higher number of ubiquitous taxa at WOH sites. Ubiquitous taxa common to both regions included generalist taxa, such as the chironomids *Eukiefferiella* spp., *Orthocladius dorenius*, and *Thienemannimyia* grp., that are tolerant of organic pollution, whereas several ubiquitous taxa in the WOH region, including *Epeorus pleuralis*, *E. vitreus*, *Ephemerella dorothea*, *E. invaria* grp., and *Baetis* spp., are intolerant of organic pollution. The WOH region probably had more ubiquitous taxa than the EOH region because anthropogenic stressors at certain EOH sites limited abundances of sensitive generalists. This point was further emphasized by the finding that among-site similarities were better maintained in the NMDS ordination of EOH sites based on common taxa >1% RA than in the NMDS ordination of WOH sites based on common taxa >1% RA. Moreover, the NMDS ordination of EOH sites based on common taxa >1% RA was better related to measured environmental gradients than the NMDS ordination of WOH sites based on common taxa >1% RA.

Rarity and the outcome of multivariate analyses

Investigations of the role of rarity in multivariate analyses usually have concentrated on exclusion of rare taxa when using traditional ordination techniques (Cao and Larsen 2001). Few studies have quantified the information contained in the rare taxa in a community (Magurran and Henderson 2003, Nijboer and Schmidt-Kloiber 2004, Nijboer and Verdonshot 2004), particularly with regard to multivariate statistical analyses (but see Faith and Norris 1989). Rare taxa can contribute noise (variability) to analyses (Bailey et al. 2004) or are redundant (Marchant 1999, 2002), and these issues have been used to justify removing rare taxa from analyses where community composition rather than richness is critical for discerning patterns.

How do commonness and rarity affect measures of among-site similarity?—Removing numerically common taxa from our data set reduced mean among-site similarity even though the number of taxa removed was small. Removing numerically rare taxa also reduced mean among-site similarity.

Rare taxa can be filtered from data sets in many ways, but the most common filter is to remove taxa that contribute <1 or 2% of the total abundance across all sites (Bailey et al. 2004). In contrast, taxa were filtered in our study by removing all taxa that accounted for <1 or 0.3% (rare) or >1 or 0.3% (common) *within* a site. These filters were intended to simulate field collection and counting decisions (i.e., analogous to fixed 100- or 300-macroinvertebrate

counts or sampling decisions) rather than a posteriori statistical decisions. The filters resulted in removal of different taxa at different sites and apparently strengthened site-specific distinctiveness relative to the overall data matrix (i.e., greater dissimilarity among sites). Our results suggest that a less-rigorous sampling effort could artificially increase dissimilarity among sites, thereby increasing type I errors (i.e., incorrectly rejecting a null hypothesis that sites are similar). The chance that this type I error could emerge depends on, among other things, the relative changes within each similarity matrix. Relative change was greater among WOH common- and rare-taxa similarity matrices (projected via NMDS) than among EOH matrices, a phenomenon we attributed to the more-subtle environmental gradients in the WOH region than in the EOH region.

Nijboer and Schmidt-Kloiber (2004) found that site-quality scores (multimetric index; Vlek et al. 2004) increased when low-abundance taxa were excluded from data sets, but site-quality scores decreased when taxa with restricted distributions were excluded from data sets. Nijboer and Schmidt-Kloiber (2004) showed that many low-abundance taxa were indicators of degradation of stream morphology and that low-abundance taxa accounted for a large portion of taxa richness, whereas many spatially rare taxa were indicators of special habitat conditions or least-impacted sites. The differing effects of abundance-based and location-based rarity ultimately led to their recommendation that a rarity metric (quantifying distributional rarity) should be included in European ecological assessment studies. A dichotomy between numerical and spatial rarity also was observed in our study in that removing spatially rare taxa from the data set caused mean among-site similarities to change little or increase slightly, whereas removing numerically rare taxa caused mean among-site similarities to decrease. However, we have not investigated the effect of removing rare species from a data set on a multimetric ecological integrity index.

Are rare and common taxa correlated with similar environmental variables?—Discussion of sampling effort (e.g., Vinson and Hawkins 1996, Doberstein et al. 2000, King and Richardson 2002, Lorenz et al. 2004), particularly as it relates to macroinvertebrate bioassessment (Barbour and Gerritsen 1996, Courtemanch 1996, Carter and Resh 2001), has focused on the number of individuals needed for robust site classifications using multimetric biological indices. Our definitions of common and rare taxa are used in bioassessment studies (1 and 0.3% RA are used to simulate 100 and 300 macroinvertebrate counts, respectively).

In the WOH region, removing numerically less-abundant taxa (particularly rare taxa 1–0.3% RA) reduced variance loading in the NMDS ordination and decreased the number and strength of significant correlations between NMDS factors and environmental variables. That is, removing rare taxa and leaving only common taxa in the data set increased the unexplained variance (noise, *sensu* Bailey et al. 2004) in the data set. Ordinations of rare-taxa data sets yielded more and stronger correlations between NMDS factors and environmental variables than ordinations of common taxa >1% RA data sets, suggesting that common taxa contributed noise to our WOH data set.

In the EOH region, removing numerically common or rare taxa from data sets caused very little change in the strengths of correlations between NMDS factors and environmental variables but slightly reduced variance loading in the NMDS ordination. Both rare and common taxa contributed information that was correlated with environmental variables (i.e., redundant information, *sensu* Marchant 1999, 2002) and neither rare nor common taxa clearly increased the unexplained variance. Faith and Norris (1989) observed that more environmental gradients were recovered in a hybrid MDS of 229 rare taxa than in an ordination of their 40 most common taxa, and they recommended retaining rare taxa in multivariate community analyses because the presumption that rare taxa did not carry additional information was unwarranted. However, Faith and Norris (1989) did not quantify unexplained variance attributed to rare taxa.

Are multivariate ordinations of rare and common taxa correlated?—All Mantel *r*-values calculated for pairwise comparisons of rare, common, and all taxa data sets were significant. However, *r*-values were lowest for comparisons between the most extreme definitions of numerical commonness (>1% RA) and rarity (<0.3% RA) ($r = 0.50$ and 0.40 for EOH and WOH data sets, respectively). Cao and Larsen (2001) suggested that rare taxa may respond to different gradients than common taxa. Inspection of our among-site NMDS ordinations and correlations with environmental variables did reveal some differences in the spatial arrangement of sites depending on whether ordinations were based on rare or common taxa (particularly for ordinations of common taxa in the WOH region). Nevertheless, these differences did not reveal stronger or more novel relationships with any of the environmental variables in our data set. It is possible that the variance expressed in these ordinations could be better explained with additional environmental variables. Nevertheless, at least using our definitions of rarity,

rare and common taxa had no distinguishable differential responses to environmental gradients. As pointed out by Marchant (2002), Faith and Norris (1989) observed a greater number of significant taxa–environment correlations when their data set included rare taxa, but the responses of rare and common taxa described a similar environmental gradient related to total dissolved solids.

Rarity and taxonomic resolution—implications for study design and data interpretation

Identifying 36% of all individuals to species in our study was an intensive and time-consuming process. Species-level identifications provided the greatest level of detail regarding taxa–environment relationships, but genus- and species-level matrices were strongly correlated. At a broad scale, biogeographic influences were apparent even at family-level taxonomic resolution using presence/absence data (Kratzer et al. 2006, DBA, unpublished data). Within biogeographic regions, collapsing taxonomic levels had a greater negative effect on among-site discriminatory power in the WOH region where environmental gradients were subtle than in the EOH region where environmental gradients were strong. However, in the EOH region, collapsing taxonomic resolution from the family to the order level decreased our ability to discriminate among highly impacted sites.

Taxonomic resolution and degree of rarity differentially affected the outcome of multivariate statistical analyses in 2 regions with differing biogeographic and anthropogenic factors. If the goal of a study is to quantify or predict differences among less-impacted sites or between moderately and highly impacted sites with potentially different stressors, then taxonomic effort should be maximized and rare taxa should be collected and retained for statistical analyses. Doberstein et al. (2000) suggested that counts of 100 to 300 ind./site might yield poor discriminatory power and mislead water-resource decision makers. Others have recommended using counts of ≥ 200 ind./site (King and Richardson 2002), but studies involving several regions or stream types may require counts of >500 (Cao et al. 2002) or even >700 ind./site (Lorenz et al. 2004). If the primary goal of a study is to distinguish severely degraded from healthy sites and financial resources are limited, family-level taxonomic resolution and counts of 100 ind./site may be appropriate. However, as water resources become less degraded in the future (a goal of environmental protection frameworks) choices made today that establish baseline descriptions with fine taxonomic resolution and robust

quantification of rare taxa will provide greater confidence when documenting temporal changes.

Temporal, spatial, and numerical rarity each accounted for nearly ½ of all of our taxonomic units. Our sampling and identification efforts resulted in counts >800 ind. site⁻¹ y⁻¹. An often unrecognized value of such a rigorous effort is its contribution to perception or perspective in the environmental education and policy arena. For example, unmodified richness estimates for our most diverse and depauperate sites were 127 and 18 taxa, respectively, a difference of 109 taxa. These sites also had the lowest and highest levels of anthropogenic stressors. Removing taxa occurring at <1% RA changes this comparison to 32 and 6 taxa, respectively, a perceived loss of only 26 taxa. Certainly the relative difference between sites is maintained, and the difference still indicates biological impairment, but filtering rare taxa severely diminishes our power to communicate the degree of loss caused by human factors.

Acknowledgements

We are indebted to Jan Battle, Andy Byler, William Crouch, Dave Funk, John Johanson, Bryan Lees, David Lieb, Will Milliken, Sally Peirson, Roberta Weber, and many interns for their tireless field work and patience during sample sorting and identification of the macroinvertebrates. Thanks to Pamela Silver, Robert C. Bailey, and an anonymous referee for their critical reviews of earlier versions of this manuscript. This research was funded by a grant under the Safe Drinking Water Act from the New York State Department of Environmental Conservation and the US Environmental Protection Agency.

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Received: 16 November 2005

Accepted: 7 July 2006