# Multilevel Assessment of Fish Species Traits to Evaluate Habitat Degradation in Streams of the Upper Midwest 

Robert M. Goldstein*<br>U.S. Geological Survey, 196 Whitten Road, Augusta, Maine 04332, USA<br>Michael R. Meador<br>U.S. Geological Survey, 12201 Sunrise Valley Drive, MS 413, Reston, Virginia 20192, USA


#### Abstract

We used species traits to examine the variation in fish assemblages for 21 streams in the Northern Lakes and Forests Ecoregion along a gradient of habitat disturbance. Fish species were classified based on five species trait-classes (trophic ecology, substrate preference, geomorphic preference, locomotion morphology, and reproductive strategy) and 29 categories within those classes. We used a habitat quality index to define a reference stream and then calculated Euclidean distances between the reference and each of the other sites for the five traits. Three levels of species trait analyses were conducted: (1) a composite measure (the sum of Euclidean distances across all five species traits), (2) Euclidean distances for the five individual species trait-classes, and (3) frequencies of occurrence of individual trait categories. The composite Euclidean distance was significantly correlated to the habitat index ( $r=-0.81 ; P=0.001$ ), as were the Euclidean distances for four of the five individual species traits (substrate preference: $r=-0.70, P=0.001$; geomorphic preference: $r=-0.69, P=0.001$; trophic ecology: $r=-0.73, P=0.001$; and reproductive strategy: $r=-0.64, P=0.002$ ). Although Euclidean distances for locomotion morphology were not significantly correlated to habitat index scores ( $r=-0.21 ; P=0.368$ ), analysis of variance and principal components analysis indicated that Euclidean distances for locomotion morphology contributed to significant variation in the fish assemblages among sites. Examination of trait categories indicated that low habitat index scores (degraded streams) were associated with changes in frequency of occurrence within the categories of all five of the species traits. Though the objectives and spatial scale of a study will dictate the level of species trait information required, our results suggest that species traits can provide critical information at multiple levels of data analysis.


Species traits include morphological, physiological, and behavioral expressions of the adaptations of biota to their environment. Thus, species traits can be used to examine relations between the fundamental ecological function of fish assemblages and their environment (Schlosser 1990; Poff 1997). In theory, the species traits of two fish assemblages would be similar if adapted to the same environmental conditions, whereas the species traits of two assemblages exposed to different environmental conditions would differ, and the differences would be correlated to the magnitude of the environmental differences.

Species traits have been used to compare fish assemblage composition under different environmental conditions. Gatz (1979) compared fish assemblages from three different drainages by using statistical differences in species traits to infer eco-

[^0]logical differences among drainages. Poff and Allan (1995) used species traits to determine differences in fish assemblages from stable and variable hydrologic regimes. Lamouroux et al. (2002) used species traits to examine ecological convergence of taxonomically different communities on two continents. Thus, a species traits approach to comparing fish assemblage composition among sites would be useful to studies of environmental degradation because it obviates differences in taxonomic composition among sites (Poff and Allan 1995).

Although species traits have recently been applied to the evaluation of environmental degradation (Porter et al. 2000; Aarts and Nienhuis 2003), questions remain about the use of species traits as a biomonitoring tool (Gayraud et al. 2003). For example, should the focus be on a traitclass (such as reproductive strategies) to examine gross-level changes in fish assemblages or individual categories within a trait-class (such as broadcast spawning behavior) to examine very
specific responses? Also, should a composite of all species traits be used to assess environmental degradation?

The goal of this study was to evaluate the use of five fish species traits (substrate preference, geomorphic preference, trophic ecology, locomotion morphology, and reproductive strategy) classified by Goldstein and Meador (2004) to assess environmental degradation in streams of the upper Midwest of the USA. Specifically, our objectives were to (1) examine changes in fish assemblages reflected by the composite of the five fish species traits along a known gradient of habitat degradation, and (2) examine changes in individual species traits and trait categories along the gradient of habitat degradation. We hypothesized that variation in species traits would be proportional to levels of habitat degradation.

## Methods

Classification of species traits.-The five fish species trait-classes (traits) used in this analysis were (1) substrate preference, (2) channel geomorphic unit preference, (3) trophic ecology, (4) locomotion morphology, and (5) reproductive strategy. The traits were selected to provide information on the structural and functional composition of fish communities. Preferences for specific substrates and channel geomorphic unit identify habitat requirements (Goldstein and Meador 2004). Trophic ecology identifies the functional characteristics and relationships involved in feeding, food sources, and energy transformation; locomotion morphology defines morphologic adaptations to current velocity and position in the water column. Reproductive strategy identifies the ecological requirements for reproduction in terms of energy (required for migration, gamete production, and reproductive behaviors before and after spawning) or substrates (nest construction).

Each of these traits has been used either individually or in limited combination in various indices of biotic integrity (IBIs) or other environmental indices. Trophic guild has been a mainstay of IBIs since their inception (Karr 1981) and is probably the most widely used species trait. The number of species in certain taxonomic groups has been used to indicate condition of fluvial geomorphology and physical habitat, such as the number of sunfish species as indicators of pool degradation and the quality of instream structures, and the number of darter species for substrate condition (Karr et al. 1986). Several alternative metrics used in IBIs involve the proportion of various re-
productive guilds (Angermeier and Karr 1986; Miller et al. 1988; Hughes et al. 1998). Response to current velocities, though infrequently used, has been applied to indicate loss of geomorphic diversity and impoundment (Petersen 1992).

Species were classified based on the category or categories within each trait that were most congruent with information derived from life history accounts and other literature sources (Hildebrand and Schroeder 1928; Scott and Crossman 1973; Wydoski and Whitney 1979; Trautman 1981; Simpson and Wallace 1982; Becker 1983; Sigler and Sigler 1987; Robison and Buchanan 1988; Sublette et al. 1990; Page and Burr 1991; Etnier and Starnes 1993; Jenkins and Burkhead 1994; Rohde et al. 1994; Mettee et al. 1996, Pflieger 1997; Ross 2001; Moyle 2002) and other sources (e.g., Breeder and Rosen 1966). The classification applies to adults, with two exceptions: (1) where only traits of juveniles are listed (e.g., some anadromous species), these are noted in the comments column; and (2) where distinct ecological and morphological differences occur between adults and juvenile stages (e.g., lampreys), both stages are listed. The species list and nomenclature follow Robins et al. (1991). An electronic file contains the list of fish species used in the present study and their classifications based on these five species traits (http://water.usgs.gov/nawqa/ecology/pubs/ index.html). Included in the electronic file are also the classifications of most North American lotic species.

Details regarding the classification of fish species based on these traits can be found in Goldstein and Meador (2004). Briefly, eight categories of substrate preference were identified based on stream bottom substrate particle size and consistency: boulders, cobble-rubble, gravel, sand, bedrock, mud, vegetation, and variable. Five categories of channel geomorphic unit preference (hereafter, geomorphic preference) were identified: pool, riffle, run, backwater, and variable. The five categories of trophic ecology were herbivore, planktivore, detrivore, invertivore, and carnivore. The six categories of locomotion morphology were cruisers, accelerators, maneuverers, benthic highvelocity huggers, benthic low-velocity creepers, and specialists. The five reproductive strategy categories were migratory, broadcaster, simple nester, complex nester-guarder, and bearer. The "variable" category in substrate and geomorphic preferences was used when more than three categories were applicable or to indicate no specific preference. Other than locomotion morphology, classi-
fications in the other four traits are not mutually exclusive. For example, a species could be both an invertivore and carnivore, prefer sand and gravel substrates and pools and backwaters as well as be a migratory simple nester.

Selection of streams.-We examined data from Goldstein et al. (2002) on fish assemblages and habitat for low-gradient streams in the Northern Lakes and Forests Ecoregion (Omernik 1987), which covers the northern parts of Michigan, Wisconsin, and Minnesota. Ecoregions generally are considered to be regions of homogeneity in ecological systems or in relations between organisms and their environment (Omernik and Gallant 1988). Agricultural and urban land uses tend to be relatively sparse in this ecoregion (Stoner et al. 1993; Goldstein et al. 2002), and the stream basins are mostly forested in conifers. Land use within 100 m of the sampling sites was primarily forest (mean, $69.4 \%$; range, $12-100 \%$ ) followed by developed (mean, $1.8 \%$; range, $0-26.2 \%$ ), pasture (mean, $3.4 \%$; range, $0-68.8 \%$ ), agriculture (mean, $2.1 \%$; range, $0-40 \%$ ), and the remainder wetlands and water (Goldstein et al. 2002). Stream degradation in this ecoregion tends to occur primarily from timber harvest, loss of riparian vegetation from recreational development, and stream channel straightening to improve drainage for agriculture. Common indicators of degradation to the streams are increases in suspended sediment, loss of geomorphic diversity, loss of substrate diversity, reductions in woody debris and instream cover, increases in water temperature, and increases in nutrients and other chemicals. This data set contained both an index of stream habitat quality for low-gradient streams and IBI scores. The habitat index is based on a set of instream and riparian variables (sinuosity, mean length of pools, frequency of bank erosion, amount of woody debris, substrate types, and wooded riparian land cover within 100 m of the stream). Thus, we could distinguish streams along a gradient of habitat deg-radation-from streams of high habitat quality characterized by fish assemblages in good condition (high habitat quality index and IBI scores) to streams of poor habitat quality characterized by fish assemblages in poor condition (low habitat quality index and IBI scores).

We used habitat quality index and IBI scores to identify 21 streams along a gradient of habitat degradation (Table 1). The stream with the highest habitat quality index and IBI scores (Hunting Creek) was designated as representative of reference conditions. The selection process used five
criteria: (1) use only low-gradient streams to correspond with the habitat index (Goldstein et al. 2002), (2) include the highest and lowest scores, (3) delete any sites where IBI and habitat scores do not correspond (i.e., some other source of degradation may be affecting the fish assemblage)there were five sites with high HI and low IBI scores, (4) delete any sites with IBI scores of 0 (there were eight), and (5) randomly select enough sites to cover the numerical range of the habitat index. In this manner, we could examine the changes in species traits that occurred along a gradient of habitat degradation as compared with conditions at our reference site.

Data analysis.-Calculation of the frequencies of species traits for each site was accomplished by developing a matrix of fish species in the assemblage (one row per species) by species trait categories ( 29 columns for all the trait categories across all five traits). Frequencies of each species trait were calculated as the sum of each column (individual categories within a species trait) divided by the total observations in the species trait (see Appendix for an example). For each species trait, Euclidean distances (Washington 1984) were calculated between the reference assemblage and each of the 20 other stream assemblages based on the frequencies of occurrence calculated for each trait. Gatz (1979) used Euclidean distance to assess differences in species traits. Euclidean distance is the square root of the sum of the paired differences squared (Clifford and Williams 1976; see Appendix for formula and calculations). In addition to the individual distances, the five Euclidean distances were summed as an overall composite statistic for further comparison.

We conducted Pearson product-moment correlation analysis to examine relations among habitat index scores, IBI scores, and Euclidean distances. We used analysis of variance (ANOVA) and Scheffé's contrasts to compare mean Euclidean distances among the five species traits in the 20 (nonreference) streams. Principal components analysis (PCA) was conducted on a correlation matrix of the species traits among the 20 nonreference sites based on their Euclidean distances for each of the five species traits to assess patterns in variation. Trait Euclidean distances were standardized (mean, 0; SD, 1) before analysis. The number of PCA axes examined was determined by Kaiser's rule, which states that the minimum eigenvalue should be 1 when correlation matrices are used (Legendre and Legendre 1983). Site scores on PCA axes (based on species traits) were related to

Table 1.-Habitat quality index scores, index of biotic integrity (IBI) scores, and Euclidean distances for five species traits from fish assemblages from streams in the Northern Lakes and Forests Ecoregion. Multiple sites were sampled on some streams. The fish assemblage from Hunting Creek was used as the reference assemblage. The composite Euclidean distance is the sum of the distances of the five species traits comparisons. Habitat index scores range from +10 (best) to -10 , and IBI scores range from 100 (best) to 0 (Goldstein et al. 2002). See text for more information on traits.

| Stream | Habitat index score | IBI score | Euclidean distance |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | Trophic composition | Substrate preference | Geomorphic preference | Locomotion morphology | Reproductive strategy | Composite |
| Hunting | 4 | 70 | Reference | Reference | Reference | Reference | Reference | Reference |
| South Fork Jump | 3 | 70 | 7.7 | 12.2 | 11.3 | 19.0 | 7.0 | 57.3 |
| West Branch Ontonagon | 3 | 55 | 10.9 | 14.2 | 15.8 | 12.3 | 15.4 | 68.7 |
| McKenzie | 1 | 65 | 10.3 | 17.1 | 14.4 | 23.6 | 6.2 | 71.6 |
| Upper Tamarack | 1 | 57 | 9.1 | 9.2 | 9.7 | 22.2 | 14.2 | 64.4 |
| Flint | -1 | 45 | 11.6 | 17.4 | 22.3 | 24.6 | 20.3 | 96.2 |
| North Fork Copper | -1 | 35 | 3.4 | 9.6 | 14.8 | 28.9 | 13.5 | 70.2 |
| Skinner | -2 | 55 | 10.5 | 13.1 | 15.4 | 19.4 | 19.7 | 78.2 |
| Anchor | -2 | 55 | 7.1 | 16.0 | 26.8 | 16.6 | 20.0 | 86.5 |
| North Fork Copper | -2 | 47 | 8.9 | 13.0 | 15.1 | 29.8 | 13.5 | 80.2 |
| Kenyon | -2 | 42 | 14.2 | 13.2 | 19.0 | 24.7 | 4.0 | 75.1 |
| Bug | -2 | 40 | 17.4 | 21.4 | 30.2 | 22.8 | 17.3 | 109.0 |
| Lower Ox | -2 | 40 | 13.1 | 9.4 | 17.6 | 19.6 | 16.3 | 76.0 |
| Ash | -2 | 35 | 13.1 | 14.3 | 14.3 | 14.0 | 18.2 | 73.9 |
| Anchor | -3 | 55 | 11.6 | 11.1 | 17.0 | 18.3 | 17.0 | 75.0 |
| Waupee | -3 | 55 | 13.9 | 15.1 | 19.0 | 28.3 | 20.7 | 97.0 |
| Fourche | -5 | 45 | 23.6 | 20.1 | 23.7 | 26.6 | 22.4 | 116.5 |
| Waupee | -5 | 45 | 14.6 | 17.5 | 18.4 | 22.2 | 22.3 | 95.0 |
| Amnicon | -6 | 30 | 18.3 | 26.9 | 33.6 | 23.6 | 20.4 | 122.8 |
| Rapid | -6 | 27 | 16.3 | 25.0 | 21.9 | 19.2 | 12.2 | 94.7 |
| Unnamed | -8 | 15 | 33.0 | 44.0 | 32.7 | 20.8 | 35.3 | 165.7 |

habitat index values using Pearson correlation analysis.

Least-squares linear regression and generalized nonlinear least-squares regression analyses were used to examine relations between habitat index scores (dependent variable) and frequencies of occurrence of individual species trait categories (independent variables). A second-order polynomial model was used for nonlinear regression. Frequencies of occurrence of species trait categories were examined for normality using normal probability plots and were transformed to improve normality by using arcsine square root. All differences were declared to be statistically significant when alpha was less than 0.05 . Significance for the correlation analyses was determined based on the Bonferroni correction for multiple pairwise comparisons and a $P$-value of less than 0.05 .

## Results

Composite Euclidean distances between nonreference stream assemblages and the reference site assemblage were negatively correlated to their
habitat index scores ( $r=-0.81, P=0.001$ ) and negatively correlated to IBI scores $(r=-0.69, P$ $=0.001$; Table 2). Index of biotic integrity scores were positively related to habitat index scores $(r$ $=0.76, P=0.001$; Table 2).

Euclidean distances for four of the five individual species traits were significantly negatively correlated to habitat index scores (substrate preference: $r=-0.70, P=0.001$; geomorphic preference: $r=-0.69, P=0.001$; trophic composition: $r=-0.73, P=0.001$; and reproductive strategy: $r=-0.64, P=0.002$; Table 2). However, Euclidean distances for locomotion morphology were not significantly correlated to habitat index scores ( $r=-0.21, P=0.368$ ). A similar pattern was observed for correlations with Euclidean distances and IBI scores (Table 2). However, Euclidean distances for locomotion morphology were not significantly correlated with Euclidean distances for any other species trait (Table 2). In contrast, Euclidean distances for the other four species traits were significantly correlated with each other.

Mean Euclidean distances for individual species

Table 2.-Pearson product-moment correlations among Euclidean distances for each of five species traits, habitat index scores, and IBI scores for the 20 nonreference assemblages. The rho values (first row for each category) of significant correlations are in bold italics. Significance was determined based on the Bonferroni correction for multiple pairwise comparisons and a $P$-value of less than 0.05 .

| Score or trait | Habitat index score | IBI score | Composite trait distance | Substrate preference | Geomorphic preference | Trophic ecology | Locomotion morphology |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| IBI score | 0.76 |  |  |  |  |  |  |
|  | 0.001 |  |  |  |  |  |  |
| Composite trait distance | $\begin{gathered} -0.81 \\ 0.001 \end{gathered}$ | $\begin{gathered} -0.69 \\ 0.001 \end{gathered}$ |  |  |  |  |  |
| Substrate preference | -0.70 | -0.67 | 0.92 |  |  |  |  |
|  | 0.001 | 0.001 | 0.001 |  |  |  |  |
| Geomorphic preference | -0.69 | -0.62 | 0.87 | 0.79 |  |  |  |
|  | 0.001 | 0.004 | 0.001 | 0.001 |  |  |  |
| Trophic ecology | -0.73 | -0.63 | 0.89 | 0.86 | 0.69 |  |  |
|  | 0.001 | 0.003 | 0.001 | 0.001 | 0.001 |  |  |
| Locomotion morphology | -0.21 | -0.08 | 0.19 | -0.01 | 0.07 | 0.02 |  |
|  | 0.368 | 0.724 | 0.421 | 0.963 | 0.774 | 0.943 |  |
| Reproductive strategy | -0.64 | -0.51 | 0.79 | 0.63 | 0.59 | 0.65 | -0.06 |
|  | 0.002 | 0.023 | 0.001 | 0.003 | 0.006 | 0.002 | 0.810 |

traits were greatest for locomotion morphology, followed in order by substrate preference, reproductive strategy, and trophic ecology (Table 3). Analysis of variance indicated that mean Euclidean distances were significantly different among the five species traits $(P=0.002$, $\mathrm{df}=4,95)$. Euclidean distances for locomotion morphology were significantly greater than distances for trophic composition ( $P=0.0003$ ), substrate preference ( $P=0.025$ ), or reproductive strategy ( $P=$ 0.01 ; Table 3). Euclidean distances for geomorphic preference were also significantly greater than distances for trophic composition $(P=0.005)$. No other significant differences were detected among the five species traits.

The PCA produced two axes with eigenvalues greater than one that together summarized $82.4 \%$
of the variation in the categories across the species traits (Table 4). The first axis had high factors loadings greater than 0.50 (in absolute value) for geomorphic and substrate preferences, and for trophic ecology, while only locomotion morphology exhibited a high loading on the second axis (Figure 1; Table 4). Reproductive strategy had similar loadings (absolute value) on both axes (Figure 1; Table 4). Habitat index scores were correlated with PCA axis 1 scores $(r=-0.71, P=0.001)$ but not with PCA axis 2 scores $(r=-0.20, P=0.410)$.

Two of the 29 species trait categories, preferences for bedrock and live-bearing species, were not present in our data (Table 5). Of the 27 species trait categories in our data, the frequencies of occurrence of 14 trait categories were significantly, linearly related to the habitat index scores, in-

TABLE 3.-Mean Euclidean distances and contrast matrix ( $P$-values from Scheffe's contrasts after analysis of variance) of Euclidean distances between a reference fish assemblage and assemblages for 20 streams in the Northern Lakes and Forests Ecoregion for five fish species traits. $P$-values in bold italics indicate statistically significant differences between the traits for those rows and columns.

| Trait | Trophic <br> ecology | Substrate <br> preference | Geomorphic <br> preference | Locomotion <br> morphology | Reproductive <br> strategy |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Trophic <br> ecology <br> Substrate <br> preference <br> Geomorphic <br> preference | 0.130 | 0.005 | 0.001 | 0.110 |  |
| Locomotion <br> morphology |  | 0.260 | 0.025 | 0.940 |  |
| Mean Euclidean <br> distance | 13.4 | 17.0 | 19.6 | 0.246 | 0.190 |

Table 4.-Principal components analysis (PCA) loadings for species traits on the first two PCA axes.

| Species trait | PCA axis 1 | PCA axis 2 |
| :--- | :---: | :---: |
| Substrate preference | 0.55 | 0.03 |
| Geomorphic preference | 0.55 | 0.02 |
| Trophic ecology | 0.51 | 0.02 |
| Locomotion morphology | 0.07 | 0.95 |
| Reproductive strategy | 0.35 | -0.30 |
| Percent variance explained by component | 62.15 | 20.27 |

cluding two or more trait categories from all traits except for reproductive strategy (Table 5). One reproductive strategy trait, simple nesters, was significantly nonlinearly related to the habitat index.

## Discussion

## Multilevel Analysis

The species traits methodology for evaluating aquatic resources quality is a combination of a guild approach (Austen et al. 1991) and various IBIs (Miller et al. 1988; Simon 1999). This modification attempts to use species traits as a "macrodescriptor" (Orians 1980) of fish assemblages without the need for local or regional modifications. Responses to environmental conditions are measured not by the response of the entire guild, a taxonomic metric, or changes in relative abun-
dance, but by the change in the life history attributes of the assemblage. The species traits approach builds from an ecological foundation with empirical relationships among the traits and environmental variables (Angermeier et al. 2000). The empirical relationships become more evident when examined across the three levels of analysis: the composite score, five individual trait scores, and the frequencies of categories within each trait.

The composite species trait distance appeared to be a useful tool for assessing changes in fish assemblage function along a gradient of habitat disturbance in streams in the Northern Lakes and Forests Ecoregion. The strength and significance of the response (absolute rho and $P$-value) of the composite distance measure were similar to those of the IBI for these streams. However, like an IBI,


PCA Axis 1
Figure 1.-Principal components analysis (PCA) plot of axes 1 and 2. The arrows indicate the species trait loadings, the circles the site loadings. Note that the arrows indicating the loadings for substrate, geomorphic preference, and trophic ecology overlap.

Table 5.-Mean frequency of occurrence of species trait categories and linear and nonlinear relations with the habitat index. Nonlinear results are based on a second-order polynomial model; the $R^{2}$ and $P$-values of significant relations are in bold italics.

| Species trait | Species trait category | Mean frequency of occurrence (\%) | Linear regression |  | Nonlinear regression |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | $R^{2}$ | $P$ | $R^{2}$ | $P$ |
| Substrate preference | Boulder | 3.2 | 0.46 | 0.001 | 0.47 | 0.003 |
|  | Cobble | 19.5 | 0.18 | 0.057 | 0.23 | 0.094 |
|  | Gravel | 25.5 | 0.53 | 0.001 | 0.71 | 0.001 |
|  | Mud | 13.1 | 0.57 | 0.001 | -0.57 | 0.001 |
|  | Sand | 21.0 | -0.01 | 0.682 | -0.28 | 0.049 |
|  | Variable | 6.5 | -0.03 | 0.487 | -0.26 | 0.071 |
|  | Vegetation | 11.2 | -0.38 | 0.003 | -0.58 | 0.001 |
| Geomorphic preference | Backwater | 15.1 | -0.19 | 0.049 | -0.21 | 0.124 |
|  | Bedrock | 0.0 |  |  |  |  |
|  | Pool | 55.0 | -0.45 | 0.001 | -0.47 | 0.003 |
|  | Riffle | 14.4 | 0.24 | 0.025 | 0.24 | 0.086 |
|  | Run | 13.4 | 0.39 | 0.002 | 0.47 | 0.003 |
|  | Variable | 2.2 | 0.20 | 0.040 | 0.21 | 0.116 |
| Trophic ecology | Carnivore | 15.5 | 0.21 | 0.038 | 0.26 | 0.066 |
|  | Detritivore | 9.6 | -0.19 | 0.049 | -0.22 | 0.102 |
|  | Herbivore | 12.8 | 0.01 | 0.791 | 0.08 | 0.628 |
|  | Invertivore | 55.9 | 0.45 | 0.001 | 0.51 | 0.002 |
|  | Planktivore | 6.2 | -0.19 | 0.051 | -0.28 | 0.126 |
| Locomotion morphology | Accelerator | 8.6 | -0.45 | 0.001 | -0.50 | 0.002 |
|  | Creeper | 21.3 | 0.06 | 0.292 | 0.14 | 0.249 |
|  | Cruiser | 40.2 | -0.05 | 0.330 | -0.08 | 0.475 |
|  | Hugger | 18.7 | 0.32 | 0.008 | 0.39 | 0.012 |
|  | Maneuverer | 10.2 | -0.02 | 0.589 | -0.22 | 0.109 |
|  | Specialist | 1.0 | -0.02 | 0.584 | -0.02 | 0.862 |
| Reproductive strategy | Bearer | 0.0 |  |  |  |  |
|  | Broadcaster | 26.9 | -0.00 | 0.983 | -0.07 | 0.517 |
|  | Complex nester | 32.4 | -0.17 | 0.063 | -0.26 | 0.070 |
|  | Migratory | 15.1 | 0.05 | 0.335 | -0.05 | 0.633 |
|  | Simple nester | 25.7 | 0.09 | 0.180 | 0.34 | 0.025 |

a composite species trait distance measure provides little insight into more specific responses of the fish assemblage or the sources or types of disturbance that have occurred and that may be driving the responses observed. The significant correlation between the composite measure and the IBI underscores the fact that both provide a similar index to fish assemblage function. While IBIs typically contain additional information about the taxonomic composition of a fish assemblage, such as species richness in different families, the inclusions of taxonomic structural metrics often require regional modifications to an IBI because of zoogeographic variation in fish taxonomic metrics (Miller et al. 1988). Since the use of species traits may be less geographically constrained than measures that rely on taxonomic-based metrics (Lamouroux et al. 2002), the use of a composite species trait measure may require little modification at broad geographic scales. However, the species traits approach means that although the ecological composition of all species in the assemblage is evaluated, the taxonomic composition is not. If,
for example, nonnative species are a source of degradation to be considered (Rahel 2002), then a species traits approach should be modified to address the contribution of the nonnative species to the assemblage. If the objectives are not related to nonnative species, then they can be considered as part of the assemblage provided they are not maintained by stocking.

A separate examination of each of the five individual traits indicated that the species trait level of analysis could provide more specific information about functional changes in fish assemblages. Results indicated that each of the five traits contributed to variation in fish assemblages along the gradient of habitat disturbance. Four of the five traits (substrate and geomorphic preferences, trophic ecology, and reproductive strategy) were related to degradation as implied by the habitat index. The remaining trait, locomotion morphology, was not related to the habitat index. This trait is based on morphological adaptations to current velocity. However, the habitat index did not contain any current velocity-related variables, so lack of
correlation to the habitat index is not surprising. Mean Euclidean distances for locomotion morphology were among the highest measured for the individual traits. This suggests that the locomotion morphology trait measured variation in fish assemblages that was not attributed to the stream degradation as indicated by the habitat index, but contained information worthy of additional evaluation. This is further evidenced by the results of the PCA where locomotion morphology had a relatively low loading on the first axis. Locomotion morphology had the highest loadings on the second axis (Table 4; Figure 1).

Rather than independent consideration of the five individual trait analyses, our results across multiple levels of analysis show that when evaluated together, these traits contain synergistic information: information that is greater than that from summing results for individual traits. The example in the Appendix (of calculating Euclidian distance) can demonstrate the information content derived from multiple levels of analysis. Examination of one trait provides a portion of the overall picture that becomes more clearly defined with the addition of information from other traits. Moreover, they suggest additional relevant questions and action needed to answer them. In this example, each of the five trait distances indicates impairment, but this was the stream with the poorest quality habitat as measured by the habitat index. What are the sources of degradation, and can they be identified from the analysis? Can species traits be used as a diagnostic tool? Each of the traits provides some information on the nature of the habitat impairment that has occurred. Trophic ecology, habitat preferences, and reproductive strategies all indicate a severe difference in the unnamed stream compared with the reference condition (compared with the other streams evaluated). Only locomotion morphology seems less affected, with a distance similar to the mean for all the streams (Table 3). While many of the streams in this region have been channelized, the combined impairments to trophic ecology, substrate preference, and reproductive strategy suggest a change in sediment size composition with a change to the geomorphic composition of the stream.

Although it is desirable to determine changes in fish assemblages based on changes in certain species traits, study objectives may require more detailed analyses at the species trait category level. Detailed analyses directed at changes in frequency distributions across categories within species traits could provide additional information as to the par-
ticular factors driving those changes that are not provided by summary statistics for the species traits. For example, the Euclidean distance for trophic ecology in the unnamed stream in the Northern Lakes and Forests Ecoregion (33.0) was much greater than the trophic ecology distances in any of the other streams (Table 1). Comparison of the frequencies from the reference to this stream (see Appendix) indicated similar frequencies of herbivores, greater frequencies of planktivores and detritivores, and reduced frequencies of the other trophic ecology categories. Within substrate preferences, there was an increased frequency for vegetation preference, and decreased geomorphic preferences for riffles and runs. The unnamed steam assemblage has gained accelerators but lost high-velocity huggers. Reproductive strategies in the unnamed stream were very different compared with those in the reference condition. Broadcasters increased as did complex nesters, while simple nesters and migrators decreased. The information provided by category frequency changes within each of the five species traits suggests a fish assemblage dominated by lentic species. Although no dam or impoundment was noted at this site (Table 6), the magnitude and types of changes in the frequencies of each of the traits support this conclusion: (1) a small-scale dam (e.g., a beaver dam) would relate to changes in trophic ecology with increased planktivores and detritivores normally associated with more lentic environments (Vannote et al. 1980; Goldstein and Meador 2004); (2) substrate preferences for mud and vegetation or lack of substrate preference indicate an increase in species which prefer lentic shorelines or are "pelagic"; (3) an impoundment would reduce riffles and increase the frequencies of pool, run, and backwater preferences; (4) an impoundment would produce low-velocity habitats, changing the locomotion morphology frequencies by reducing high velocity huggers and producing low-velocity areas for accelerators; and (5) complex nesters tend to require low velocity or velocity protection for nests, and dams reduce migrators.

## Applications and Potential Modifications

The objectives of a project or study will dictate the necessary level or levels of information required. In this example, a resource manager might view the composite score as an indication of resource quality degradation in the unnamed stream. The five individual species traits analyses would also provide specific information regarding functional impairment. Comparison of the category

Table 6.-Comparison of stream and riparian habitat between Hunting Stream and an unnamed stream (for definitions of habitat characteristics, see Goldstein et al. 2002).

| Characteristic | Hunting | Unnamed |
| :--- | :---: | :---: |
| Basin area $\left(\mathrm{km}^{2}\right)$ | 66 | 9 |
| Width (m) | 18.8 | 3.3 |
| Depth (m) | 0.3 | 0.1 |
| Length sampled (m) | 288 | 150 |
| Land use within 100 m (\%) |  |  |
| Wooded | 84.6 | 15.7 |
| Shrubs | 11.9 | 26.9 |
| Meadow | 0 | 56.1 |
| Wetland | 1.9 | 0 |
| Other | 1.5 | 1.1 |
| Bank erosion (\%) | 2.7 | 0 |
| Substrate composition (\%) |  |  |
| Detritus | 8.3 | 0 |
| Silt | 11.1 | 62.3 |
| Sand | 20.2 | 33.3 |
| Gravel | 35.6 | 0 |
| Rubble | 12.6 | 0 |
| Boulder | 12.1 | 0 |
| Clay | 0 | 4.4 |
| Embeddedness (\%) | 37 | 100 |
| Geomorphology |  |  |
| Gradient (m/km) | 1.9 | 0.6 |
| Sinuosity | 1.1 | 2.2 |
| Mean pool length (m) | 0 | 60 |
| Mean riffle length (m) | 27 | 0 |
| Mean run length (m) | 52 | Not |

${ }^{\text {a }}$ Sinuosity is the ratio of the channel length between two points and the straight-line distance between those points.
frequencies would provide the diagnostics to allow the manager to identify a course of action for remediation or restoration. The manager could then follow the progress of the recovery by using a monitoring or trends program.

In the present study, not all responses were linear. Most previous multimetric evaluations have assumed linear responses between degradation and the index (Karr et al. 1986). Mebane et al. (2003) found nonlinear responses between IBI metrics and degradation in Pacific Northwest rivers. Unfortunately, the interactions of physical and chemical degradation at varying levels do not always produce simple responses, so the more information that is available, the clearer the picture will become. Additional classifications within traits and multiple classifications within traits are two options for increasing information. It may be that additional classifications may be needed within some of the traits. For example, geomorphic preference was established with general fluvial habitats. Given the variability in pool, riffle, and run depths and velocities, an additional classification based on combinations of depths and velocity
(e.g., slow-shallow, slow-deep, fast-shallow, and fast-deep) within each geomorphic unit might provide additional insight. Multiple classifications within traits also increase information. The classification of a species into multiple trophic categories is indicative of the variability in feeding ecology and preferable to a generalist classification of omnivore, whereby the scope and variability in feeding ecology is lost (Goldstein and Simon 1999). However, to classify species into multiple-trait categories requires life history information which may be limited for certain species traits, such as reproductive strategies (Goldstein and Meador 2004).

The management applications of species traits comparisons are potentially numerous. Species traits analysis could be used for evaluations of resource quality extending beyond habitat, stream and river fisheries (evaluating the potential for establishing new stream fisheries or diagnosis of populations that are not performing to expectations), fish community monitoring and assessment, and evaluating the potential effects of new introductions. For all these applications the basic ap-
proach is similar: define the initial or reference community and make comparisons of the frequencies in each of the species trait categories. For resource quality evaluations, reduced frequencies in any of species traits categories should indicate which resource component is deficient or a limiting factor. For evaluating stream and river fisheries, the optimal species trait frequencies from wellestablished fisheries may be used as a reference for selecting species for stocking or for determining why a particular species is not performing well in a given stream. For long-term community or population monitoring, species traits analysis may provide a context for population fluctuations. Using a species traits analysis may determine the potential success or problems from large-scale environmental actions, such as the removal of major dams. Comparisons of the differences in the frequencies of species traits from before and after dam removal could indicate which resources will be the most problematic for reestablishing anadromous or migratory species.

There are at least three future considerations for applications of the species traits approach. The first is an evaluation of the effects of using relative abundance for weighting trait category frequencies. Using relative abundance to weight the frequencies in each category should add greater accuracy. However, weighting by relative abundance should be tested with additional studies to determine any improvements in accuracy. Testing of weighted frequencies should also extend to areas with different fish species to determine the applicability across zoogeographic regions. A second consideration is the effect of deleting rare species. Rareness can result from either low abundances or very limited distributions. While data editing is done for various multivariate procedures (Gauch 1982), Nijboer and Schmidt-Kloiber (2004) found that rare species should be included in ecological assessments. The third consideration is the evaluation of the various methods for determining reference communities.

In this study, we used a single reference community for the demonstration of the methodology. Although we justified using a single reference site because all the streams were from the same ecoregion with similar climate, geology, soils, and watersheds with similar natural vegetation (Hughes et al. 1986), we do not recommend a single reference site. Where available, numerous reference sites should be used to determine mean frequencies of traits for reference conditions. The objectives and geographical scope will affect the
method of reference site selection. If the objective of the study is similar to those where an IBI is used to examine the effects of a gradient of degradation (e.g., agriculture or urbanization) on resource quality by evaluating the fish communities, then those streams in basins with the least amount of the land use in question could be used as the reference or control sites.

As the geographic scale increases, the need for additional reference sites increases, particularly as ecoregion and zoogeographic boundaries are surpassed. One approach to establishing reference conditions for large geographic areas is to perform a species traits analysis for the ichthyofauna of the region. This is the approach used in Goldstein and Meador (2004) to compare species traits in streams of different sizes across the eastern half of the United States. In this analysis, all species from the region were classified by their species traits and by their stream size preference (e.g., found in small streams, small rivers, medium rivers, or in large rivers). All species that are found in small rivers, for example, are used to determine the frequencies of the trait categories for all small rivers in the region. This provides a fundamental species traits composition for all streams of the same size. The concept (untested) is that the frequency of species trait categories across all species in the region is related to the availability of the resources in the region that correspond to each trait category. The frequency distribution of the trait categories may not be the classical, pristine reference conditions, but they do provide a control or yardstick for comparison.

## Conclusions

The objectives and spatial scale of a study will dictate the necessary level or levels of information required. Our results suggest that a composite species trait distance measure may provide a useful tool for assessing water resource degradation at large geographic scales where IBIs have not been developed or where existing IBIs require modification because of zoogeographic influences on taxonomic metrics. Analyses based on individual species traits would also provide information regarding specific functional impairment. Comparison of trait category frequencies could allow investigators to examine relations between potential sources of degradation and specific functional responses, and thereby provide information that could lead to a course of action for remediation or restoration.

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## Appendix: Species Trait Frequency Calculation

To calculate species trait frequencies, proceed as follows:
(1) List the species in each of the two assemblages to be compared;
(2) Identify the appropriate categories within each trait for each species;
(3) Determine the frequency of each category within each trait across the entire assemblage;
(4) Compute the Euclidean distance

$$
d=\left[\sum\left(X_{i j}-X_{i k}\right)^{2}\right]^{1 / 2}
$$

to compare the frequencies of the categories within each of the groups. In this formulation,
$X_{i j}$ is the requency of a species trait category in the reference assemblage and $X_{i k}$ is the frequency of that species trait category in the assemblage from the stream being evaluated.

## Example of Determining Frequencies

Table A. 1 presents fish assemblage data for Hunting Stream (18 species), which represents the reference conditions, and the unnamed stream discussed in the text ( 6 species). The $X$ s indicate the categories of each trait that apply to the different species.

The first step in determining the frequency of each category in each trait is to sum all of the observations in each trait column. For example,

Table A.1.-Example of the determination of frequencies for each of five species traits for comparison of two fish assemblages, namely, Hunting Stream (from Table 1), which is used as a reference, and the unnamed stream from Table 1, which is compared with it in terms of Euclidean distance. Abbreviations are as follows: $\mathrm{H}=$ herbivore, $\mathrm{P}=$ planktivore, $\mathrm{D}=$ detritivore, $\mathrm{I}=$ invertivore, and $\mathrm{C}=$ carnivore (trophic); $\mathrm{BE}=$ bedrock, $\mathrm{BO}=$ boulder, $\mathrm{CO}=$ cobblerock, $\mathrm{GV}=$ gravel, $\mathrm{SA}=$ sand, $\mathrm{MD}=\operatorname{mud}$ (silt, clay, detritus), $\mathrm{VG}=$ vegetation, and $\mathrm{VR}=$ variable (substrate); RF $=$ riffle, $\mathrm{PO}=$ pool, $\mathrm{RN}=$ run (main channel), $\mathrm{BW}=$ backwater, and $\mathrm{VR}=$ variable (geomorphic); $\mathrm{CR}=$ cruiser, $\mathrm{AC}=$ accelerator, $\mathrm{HG}=$ high-velocity hugger, $\mathrm{CP}=$ low-velocity creeper, $\mathrm{MV}=$ maneuverer, and $\mathrm{SP}=$ specialist (locomotion); $\mathrm{MG}=$ migratory, $\mathrm{BD}=$ broadcaster, $\mathrm{SN}=$ simple nester, $\mathrm{CG}=$ complex nester-guarder, and $\mathrm{BR}=$ bearer (reproduction).

| Stream and species | Species traits |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Trophic |  |  |  |  | Substrate |  |  |  |  |  |  |  |
|  | H | P | D | I | C | BE | BO | CO | GV | SA | MD | VG | VR |
| Hunting (reference) |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Common shiner Luxilus cornutus |  |  |  | X |  |  |  |  | X | X |  |  |  |
| Hornyhead chub Nacomis biguttatus | X |  |  | X |  |  |  | X | X |  |  |  |  |
| Blackchin shiner Notropis heterodon |  |  |  | X |  |  |  |  |  | X |  | X |  |
| Fathead minnow Pimephales promelas |  |  | X | X |  |  |  |  |  | X | X |  |  |
| Blacknose dace Rhinichthys obtusus |  |  |  | X |  |  |  | X | X |  |  |  |  |
| Longnose dace $R$. cataractae |  |  |  | X |  |  | X |  | X |  |  |  |  |
| Creek chub Semotilus atromaculatus |  |  |  | X | X |  |  | X |  | X |  |  |  |
| White sucker Catostomus commersonii | X |  | X | X |  |  |  | X | X |  |  |  |  |
| Northern hog sucker Hypentelium nigricans | X |  |  | X |  |  |  | X | X |  |  |  |  |
| Brown trout Salmo trutta |  |  |  | X | X |  |  | X | X | X |  |  |  |
| Brook trout Salvelinus fontinalis |  |  |  | X | X |  |  | X | X | X |  |  |  |
| Brook stickleback Culaea inconstans |  | X |  | X |  |  |  |  |  |  |  |  | X |
| Mottled sculpin Cottus bairdii |  |  |  | X |  |  | X | X | X |  |  |  |  |
| Rock bass Ambloplites rupestris |  |  |  | X | X |  |  | X | X |  |  | X |  |
| Bluegill Lepomis macrochirus |  |  |  | X |  |  |  |  |  |  |  | X | X |
| Johnny darter Etheostoma nigrum |  |  |  | X |  |  |  |  |  | X | X |  |  |
| Blackside darter Percina maculata |  |  |  | X |  |  |  |  | X | X |  |  |  |
| Logperch P. caprodes |  |  |  | X |  |  |  |  | X | X |  |  |  |
| Column totals | 3 | 1 | 2 | 18 | 4 | 0 | 2 | 9 | 12 | 9 | 2 | 3 | 2 |
| Percent frequency | 11 | 4 | 8 | 65 | 14 | 0 | 5 | 23 | 31 | 23 | 5 | 8 | 5 |
| Unnamed stream |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Common carp Cyprinus carpio |  |  | X | X |  |  |  |  |  |  |  | X | X |
| Fathead minnow |  |  | X | X |  |  |  |  |  | X | X |  |  |
| Northern redbelly dace Phoxinus eos |  | X |  | X |  |  |  |  |  |  | X | X |  |
| White sucker | X |  | X | X |  |  |  | X | X |  |  |  |  |
| Central mudminnow Umbra limi |  |  |  | X |  |  |  |  |  |  | X | X |  |
| Brook stickleback |  | X |  | X |  |  |  |  |  |  |  |  | X |
| Column totals | 1 | 2 | 3 | 6 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 3 | 2 |
| Percent frequency | 8 | 16 | 25 | 50 | 0 | 0 | 0 | 9 | 9 | 9 | 27 | 27 | 18 |

Table A.2.-Example of the calculation of Euclidean distances for species traits between assemblages from Hunting Stream and an unnamed stream from Table 1. See Table A. 1 for abbreviations. Final distances may not exactly match those in Table 1 due to rounding.

| Variable | Species traits |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Trophic |  |  |  |  | Substrate |  |  |  |  |  |  |  | Geomorphic |  |
|  | H | P | D | I | C | BE | BO | CO | GV | SA | MD | VG | VR | RF | PO |
| Percent frequency |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Hunting | 11 | 4 | 9 | 65 | 14 | 0 | 5 | 23 | 31 | 23 | 5 | 8 | 5 | 19 | 46 |
| Unnamed | 8 | 16 | 25 | 50 | 0 | 0 | 0 | 9 | 9 | 9 | 27 | 27 | 18 | 11 | 67 |
| $X_{i j}-X_{i k}$ | 3 | -12 | -18 | 15 | 14 | 0 | 5 | 14 | 22 | 14 | -22 | -19 | -13 | 8 | -21 |
| $\Sigma\left(X_{i j}-X_{i k}\right)^{2}$ |  |  | 898 |  |  |  |  |  |  | 1,915 |  |  |  |  | 70 |
| Euclidean distance ${ }^{\text {a }}$ |  |  | 30.0 |  |  |  |  |  |  | 43.6 |  |  |  |  |  |

[^1]Table A.1.-Extended.

| Species traits |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Geomorphic |  |  |  |  | Locomotion |  |  |  |  |  | Reproduction |  |  |  |  |
| RF | PO | RN | BW | VR | CR | AC | HG | CP | MV | SP | MG | BD | SN | CG | BR |
|  | X | X |  |  | X |  |  |  |  |  |  |  | X |  |  |
| X | X |  |  |  | X |  |  |  |  |  |  |  | X |  |  |
|  | X |  |  |  | X |  |  |  |  |  |  | X |  |  |  |
|  | X |  |  |  | X |  |  |  |  |  |  |  |  | X |  |
|  | X | X |  |  |  |  | X |  |  |  |  |  | X |  |  |
| X |  |  |  |  |  |  | X |  |  |  |  | X |  |  |  |
|  | X |  |  |  | X |  |  |  |  |  |  |  | X |  |  |
| X | X |  |  |  |  |  | X |  |  |  | X | X |  |  |  |
| X |  | X |  |  |  |  | X |  |  |  |  | X |  |  |  |
|  |  |  |  | X | X |  |  |  |  |  | X |  | X |  |  |
|  |  |  |  | X | X |  |  |  |  |  | X |  | X |  |  |
|  | X | X |  |  |  |  |  |  | X |  |  |  |  | X |  |
| X |  | X |  |  |  |  | X |  |  |  |  |  |  | X |  |
|  | X |  | X |  |  |  |  |  | X |  |  |  |  | X |  |
|  | X |  |  |  |  |  |  |  | X |  |  |  |  | X |  |
|  | X |  |  |  |  |  |  | X |  |  |  |  |  | X |  |
|  | X |  |  |  |  |  |  | X |  |  | X | X |  |  |  |
|  |  |  |  | X |  |  |  | X |  |  |  | X |  |  |  |
| $5$ | 12 | $4$ | $2$ | $3$ | $7$ | $0$ | $5$ | $3$ | $3$ | $0$ | $4$ | $6$ | 6 | 6 | 0 |
| 19 | 46 | 15 | $8$ | 12 | 39 | $0$ | 28 | 17 | 17 | 0 | 18 | 27 | 27 | 27 | 0 |
|  | X |  |  |  |  |  |  | X |  |  |  | X |  |  |  |
|  | X |  |  |  | X |  |  |  |  |  |  |  |  | X |  |
|  | X |  |  |  | X |  |  |  |  |  |  | X |  |  |  |
| X | X |  |  |  |  |  | X |  |  |  | X | X |  |  |  |
|  | X |  | X |  |  | X |  |  |  |  |  |  |  | X |  |
|  | X |  | X |  |  |  |  |  | X |  |  |  |  | X |  |
| $1$ | 6 | $0$ | 2 | $0$ | $2$ | $1$ | $1$ | 1 | 1 | 0 | $1$ | 3 | 0 | 3 | 0 |
| 11 | 67 | 0 | 22 | 0 | 33 | 17 | 17 | 17 | 17 | 0 | 14 | 43 | 0 | 43 | 0 |

Table A.2.-Extended.

| Variable | Species traits |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Geomorphic |  |  | Locomotion |  |  |  |  |  | Reproduction |  |  |  |  |
|  | RN | BW | VR | CR | AC | HG | CP | MV | SP | MG | BD | SN | CG | BR |
| Percent frequency |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Hunting | 15 | 8 | 12 | 39 | 0 | 28 | 17 | 17 | 0 | 18 | 27 | 27 | 27 | 0 |
| Unnamed | 0 | 22 | 0 | 33 | 17 | 17 | 17 | 17 | 0 | 14 | 43 | 0 | 43 | 0 |
| $X_{i j}-X_{i k}$ | 15 | -14 | 12 | 6 | -17 | 11 | 0 | 0 | 0 | 4 | -16 | 27 | -16 | 0 |
| $\Sigma\left(X_{i j}-X_{i k}\right)^{2}$ |  | 1,070 |  |  |  |  |  |  |  |  |  | 1,257 |  |  |
| Euclidean distance |  | 32.7 |  |  |  |  |  |  |  |  |  | 35.4 |  |  |

there are 28 observations in the trophic traits category for the species from Hunting Stream. From this the individual category frequencies can be derived. For example, the frequency of herbivores is $10.7 \%$ ( $3 / 28$, which is rounded to 11 in the table); similarly, the frequency for planktivores is $3.6 \%$ ( $1 / 28$ ), that for detritivores $7.1 \%$ (2/28), that for invertivores $64.5 \%$ ( $18 / 28$ ), and that for carnivores $14.3 \%$ (4/28).

## Calculating Euclidean Distance

The first step in determining the Euclidean distance (Table A.2) is to calculate the value of $X_{i j}$ $-X_{i k}$ for each trait in category $i$. This entails subtracting the percent frequency for the unnamed stream from that for Hunting Stream. In this example, the results would be 3 for the herbivores, -12 for the planktivores, -18 for the detri-
tivores, 15 for the invertivores, and 14 for the carnivores. Each of these values would then be squared and the values summed. In this example, the sum for trophic ecology would be $898\left[3^{2}+\right.$ $\left.(-12)^{2}+(-18)^{2}+15^{2}+14^{2}\right]$; similarly, the value for substrate preference would be 1,915 , that for geomorphic preference 1,070 , that for locomotion morphology 446, and that for reproductive strategy 1,257.

The Euclidean distance between the assemblages for each of the five groups is the square root of the sum. In this example it would be 30.0 for trophic ecology, 43.6 for substrate preference, 32.7 for geomorphic preference, 21.2 for locomotion morphology, and 35.4 for reproductive strategy. The range of values for Euclidean distance would be 0 (all traits have equal frequencies) to 141.4 ( $100 \%$ frequencies in two different categories from each assemblage).


[^0]:    * Corresponding author: goldstei @usgs.gov

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[^1]:    ${ }^{\mathrm{a}}\left[\left(X_{i j}-X_{i k}\right)^{2}\right]^{1 / 2}$.

