Using Community-Level Analyses to Identify Dietary Patterns for Species in Space and Time

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ABSTRACT

Non-parametric, multivariate analyses commonly used to characterize spatial and temporal patterns in the taxonomic composition of ecological communities can likewise be useful when applied to data generated from the examination of gut contents. A suite of analyses including non-metric multidimensional scaling (NMS), multi-response permutation procedures (MRPP), and indicator species analysis (ISA) revealed interesting dietary shifts that occurred across individuals of emerald shiner (*Notropis atherinoides*) collected from among different habitats and two different time periods (pre- and post-impoundment of the upper Tombigbee River). These patterns were delineated from data that exhibited non-linear distribution and that incorporated measurements made at different scales, two factors that confound traditional parametric analyses. NMS ordination provided clear, graphic representation of the separation that occurred when *N. atherinoides* diets were viewed across space and time. MRPP analysis validated that the observed separation was statistically significant, and ISA complemented these other two analyses by identifying diet contributors that were indicative of each grouping.

INTRODUCTION

In his foundational paper, "The Lake as a Microcosm," Forbes (1887) used qualitative assessments of gut contents to illustrate linkages among various organisms in glacial lakes of the Midwestern United States. Subsequent researchers have used such trophic linkages to characterize species' life histories, construct community food webs, and trace energy flow through ecosystems. The relationship between a consumer and a particular diet item as determined through examination of gut contents typically is quantified by presence/absence, number of individuals occurring, or percentage of contribution in terms of numbers, biomass, or volume (Bowen 1996). Additionally, the different taxonomic groups present within the diet represent the diversity of trophic linkages for a particular species at a given habitat and time, although quickly digested materials may be underrepresented (Bowen 1996).

The trophic relations of a species can vary spatially and temporally, resulting in contradictory characterizations among studies reporting results from individual systems or time periods (Altig et al. 2007). Describing these patterns graphically and statistically is potentially insightful. Stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$ have been used widely to show shifts in general resource use and trophic position and allow for testable hypotheses concerning causal mechanisms (Fry 2006). These signatures are representative of the assimilation of various materials through time, making a high degree of taxonomic resolution difficult to attain with regards to specific diet contributors. Therefore, description of gut contents is often employed as a complementary measure (Michener and Schell 1994).

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Direct examination of ingested material should allow for more resolute identification of various food resources. However, identification and presentation of spatial and temporal patterns are plagued by complicating factors, including: (1) graphic presentation of multiple linkage shifts across a large number of diet contributors is difficult; (2) large, multivariate data sets that result may violate assumptions of traditional parametric analyses; and (3) the prevalence of individual diet items often is measured at different scales. A couple of options include presenting the data in tabular form and discussing variation qualitatively, or one or two principle diet contributors can be arbitrarily selected according to their prevalence and changes in their consumption analyzed using univariate techniques.

Alternatively, multivariate ordination techniques have been employed where consideration of a variety of diet contributors is desired. Saint-Jacques et al. (2000) used correspondence analysis (CA) to summarize among-individual variation in the diets of white sucker (*Catostomus commersoni*). A simple graphic assessment of the overlap between the diets of *C. commersoni* and resource availability was produced when results from the dietary CA were related to those from a parallel CA assessing the biomass of various invertebrates found in sediment cores. Sample units, individual diets here, were separated along two gradients - the contribution of benthic taxa to the diet and the contribution of zooplankton to the diet.

The potential to recognize multiple dietary gradients is an advantage to collectively considering diet contributors through the evaluation of gut contents highlighted by Saint-Jaques et al. (2000). Correspondence analysis is considered an applicable technique when a single gradient separating sample units is anticipated (Noy-Meir and Whittaker 1977). However, the use of CA is not recommended when sample units may be separated along multiple gradients because later axes are usually quadratic distortions of the first, rendering them ecologically un-interpretable (McCune and Grace 2002, Ludwig and Reynolds 1998).

Non-linear ordination techniques are robust to such data (Minchin 1987, Austin 1985) and have been similarly applied. West et al. (2003) used non-metric multidimensional scaling (NMS), a non-linear ordination technique, to identify feeding guilds for estuarine fishes where species with similar diet content clustered within ordination space. NMS also graphically revealed spatial and temporal variation in the diets of individual species. Additional analyses that validate separation among clusters, describe diet breadth under recognized conditions, and identify taxa that are indicative of diet clusters would be complementary to NMS and allow for a more detailed description of dietary variation.

We propose a suite of non-parametric community level analyses that expand upon the previously employed NMS ordination technique. For analyzing spatial and temporal patterns in diets, we provide as an empirical example the diet of a trophic generalist occurring within multiple habitats of a recently modified river system.

METHODS AND MATERIALS

Study system and model organism

A large-scale navigation and excavation project completed during the early 1980s considerably altered the Tombigbee River, impounding 300 km of its south-flowing course and connecting it via canal to the historically separate Tennessee River Drainage. The project created the Tennessee-Tombigbee Waterway (TTW) in northeastern Mississippi and west central Alabama. This alteration created novel habitats in the system as well as a corridor for the exchange of fauna between the two historically isolated systems. Among the isolated tributary rivers and streams in the TTW system are an assortment of reservoirs, artificial canals, dredged river channels, and cut-off bendways. The overwhelming trend of change in the system was a conversion of lotic

habitat to lentic, barge-friendly waters. Following this large-scale disturbance, physical habitat, consumer relationships, and food resources in the TTW system were altered (Roberts et al. 2007).

The emerald shiner (*Notropis atherinoides*) has occurred naturally within the Tombigbee River from prior to its modification through the present. Under pre-TTW conditions, this relatively small minnow was found throughout open areas of the main channel and large tributaries (Boschung 1989). Presently, we have collected it from three general habitats - the modified main channel, side-channel habitats in the form of cut-off bendways of the historic river channel, and relatively free-flowing tributaries. *Notropis atherinoides* is also known to feed on a wide variety of diet items (Ross 2001), making it an excellent model organism when attempting to describe spatial and temporal diet patterns.

Individuals of *N. atherinoides* were collected from numerous tributary, waterway and side-channel reaches within the system during summer months of 2002-2005, using a combination of seining and backpack electro-fishing. Stream flow at collection localities ranged from 0.3 to 1.03 m/s at tributary localities and 0.02 to 0.23 m/s at waterway localities and was approximately zero at side-channel localities. Fishes collected in the field were euthanized using MS-222 and fixed using 10% formalin. These later were transferred to 70% ethanol and stored until processing in the laboratory. Specimens collected from the main channel prior to waterway construction were obtained from the Mississippi Museum of Natural Science. These historical collections were obtained also during summer months and occurred at or near the sites of contemporary collections. Tributary, waterway, side-channel, and historical groups included 29, 24, 25, and 18 individuals respectively and collectively represented 26 different collections.

In order to characterize food habits, specimens were eviscerated and gut contents were transferred to a Petri dish for viewing. Viewing gut contents as a whole facilitated the identification process as individual invertebrates were often present as fragmented parts, a trait common in gut contents of minnows, which often masticate food items using pharyngeal teeth (Bond 1996). Diet contributors represented by definable individuals present within the first third of the digestive tract (i.e., from mouth to anus) were identified to order or family and enumerated. Amorphous materials was categorized as surface film material (primarily diatoms) or non-diatom plant material and dried to a constant weight. Incorporating data measured at these differing scales allowed us to include all diet materials in the data matrix, whereas extremely light-weight items (e.g., zooplankton families represented by few individuals) would have to be excluded if only weights were used, and amorphous material could not be accounted for by number of individuals.

Data analyses

A number of issues arise upon examination of our raw data that limit the possibilities for graphic representation or statistical analysis. First, *N. atherinoides* consumed a total of 60 different diet items according to our classification criteria, a number that renders visual representation and univariate statistical analysis of diet variability cumbersome. Second, diet item abundance distributions indicated that many taxa were present in the gut contents of only a few individuals within a group. Finally, the prevalence of individualistic and amorphous materials was measured according to different scales. These problems confound traditional parametric multivariate analyses that assume multivariate normality or homogeneity of variances (McCune and Grace 2002). We suspect that these complications are common in dietary data, and we thus present three complementary analyses that are robust to these problems and better capitalize on the relatively high degree of taxonomic resolution possible through the examination of gut contents.

1) *Non-metric multidimensional scaling* (NMS; Mather 1976, Kruskal 1964) was used to highlight gradients in diet composition across historical, tributary, waterway, and side-channel groups. NMS is an ordination technique most often employed by community ecologists to order sampling localities (i.e., the sample unit) with differing species compositions along environmental gradients (Ludwig and Reynolds 1988). The technique is based on an iterative search algorithm that minimizes departure from monotonicity in the relationship between dissimilarity in the original data matrix and distances in the reduced ordination space (McCune and Grace 2002). Here we consider individual *N. atherinoides* as our sample units and order them along axes describing variation in the taxonomic composition of diets. Thus, distances between sample units plotted in ordination space represent a degree of dietary dissimilarity. Sørensen distances were computed among all sample units and we followed the general NMS procedure outlined by McCune and Grace (2002).

NMS is an appropriate tool considering our data because it is robust to non-normal and non-linear data as well as issues of scale (Clarke 1993). However, results can be influenced by data transformation, and these should be done with respect to the hypothesis in question (McCune and Grace 2002). We square root-transformed our data in order to apply compression to higher values in the raw data set. This was desirable to preclude numerically dominant diet contributors from masking dietary shifts incorporating less abundant taxa. Additionally, we relativized column values according to their respective maximum row values, using $b_{ij} = x_{ij}/xmax_j$, where rows (i) are individual *N. atherinoides* and columns (j) are diet items. This reduced scale-imposed distances between the prevalence of individualistic and amorphous materials that were recorded as whole numbers and fractions of a gram, respectively.

While this data transformation and relativization can increase the amount of information garnered from a data set, they can reduce monotonicity between dissimilarity in the original data matrix and distances in the ordination space. Departure from monotonicity is measured as stress (Kruskal 1964), and at relatively high levels, ordinated distances may not accurately reflect differences in the original matrix. Various methods for evaluating stress exist (McCune and Mefford 1999, Clarke 1993, Kruskal and Wish 1978, Kruskal 1964). For ordinations conducted using PC-ORD software version 4.01 (MjM Software, Gleneden Beach, Oregon) such as presented here, values > 20 should be interpreted with caution (McCune and Grace 2002). However, some flexibility should be exercised when interpreting stress values, as stress tends to be positively associated with sample size (Clarke 1993).

A Monte Carlo procedure can be conducted to determine if NMS is extracting stronger axes than expected by chance (McCune and Grace 2002). Here, the P-value represents the probability of randomly getting a stress value equal to or less than what is observed in the NMS ordination. The Monte Carlo procedure can facilitate interpretation of the NMS axes, but it is sensitive to a number of factors including the presence of a large number of zeros in the data set (McCune and Grace 2002). This may render it not applicable to many matrices constructed from dietary data.

2) We tested for significant pair-wise and across-group differences in diet composition using *multi-response permutation procedures* (MRPP; Mielke and Berry 2001, Mielke 1984). Unlike parametric tests used for this purpose (e.g., discriminant function analysis), MRPP makes no distributional assumptions (Smith 1998). Here, a distance matrix is calculated using any of a number of possible distance measures. When MRPP is used in conjunction with NMS, it is recommended that the same distance measure be maintained across analyses (McCune and Grace 2002). Thus, our data were square-root transformed prior to analysis, and we utilized the Sørensen distance measure.

Probability of type I error is calculated using a randomization algorithm that

allows for comparison between an observed δ (weighted mean within-group distance) and the randomized δ distribution. See Mielke (1984) for a discussion of weighting options. This probability value expresses the likelihood of generating a random δ smaller than the observed value. An effect size A can also be calculated as: $A = 1 -$ observed δ/expectedδ. Representing "chance corrected within-group agreement" (McCune and Grace 2002), A is a measure of observed within-group homogeneity relative to what can be expected by chance. For our purposes, this is a measure of the overall dietary agreement among *N. atherinoides* individuals feeding under the environmental conditions present within each of the groups that we designated. Within-group homogeneity is greater than the random observation when $A > 0$ and less when $A < 0$. The A-value is useful in attaching ecological significance to observed differences among groups because it is independent of sample size (McCune and Grace 2002, Mielke 1984).

3) *Indicator species analysis* (ISA; Dufrêne and Legendre 1997) was then used to identify taxa that were indicative of *N. atherinoides* diet for each group. This analysis is free of the limiting assumptions inherent in other analyses that may be applied to this purpose because groupings are not based on a CA ordination (e.g., as in TWINSPAN) (Dufrêne and Legendre 1997). It is robust to nonlinearity and exhibits a superior ability to identify secondary gradients (Dufrêne and Legendre 1997). ISA emerges as a rigorous analytical option when investigating dietary patterns (Pierre Legendre, University of Montreal Department of Biological Sciences, pers. comm.).

ISA complements MRPP by describing the value of individual variables (each diet contributor) for separating groups. An indicator value is provided that is representative of the concentration of taxon abundance and the fidelity of a taxon to a particular group (McCune and Grace 2002). Thus, an ideal indicator for a diet group is always present in the diet of consumers from that group and is exclusive to the diet of consumers from that group. ISA yields an indicator value for each diet contributor ranging from zero (no indication) to 100 (perfect indication). Significance is tested using a Monte Carlo procedure (Fortin and Gurevitch 1993) that randomly reassigns sample units to each group through 1000 permutations. We followed the general ISA procedure outlined in McCune and Grace (2002). All aforementioned analyses were conducted using PC-ORD software, version 4.01 (MjM Software, Gleneden Beach, Oregon).

RESULTS

NMS ordination of *N. atherinoides* diets highlighted three gradients that cumulatively captured 50.0 % of the information in the analytical data set. Individuals were separated primarily along gradients describing contributions from zooplankton, plant material, or emerging nematoceran midges. Further insight was garnered when symbols categorizing individuals as collected from either historical, tributary, side-channel, or waterway conditions were overlaid on a plot displaying these individuals' locations in the three dimensional ordination space (Fig. 1). Most strongly separated were historical and waterway individuals. Using the NMS axes as a reference, waterway individuals exhibited relatively large contributions from zooplankton, while those feeding under historical conditions received greater contributions from emerging midges. Individuals feeding in side-channel habitats were separated from others because they incorporate larger amounts of plant material in their diet. Interestingly, tributary individuals were more dispersed but generally occupied an intermediate position within ordination space.

MRPP indicated that diet composition varied across all groups ($A = 0.203$, P < 0.0001). Pair-wise comparisons corroborated results obtained using NMS (Fig. 2). Most strongly separated were diets occurring under historical and waterway conditions, while tributary diets exhibited less within-group agreement and were less discretely separated

from other diets. All pair-wise comparisons were significant using an α of 0.05 after Bonferroni correction for multiple pair-wise comparisons.

ISA corroborated results from the NMS ordination in that water-column dwelling zooplankton were identified as indicators of the waterway diet. However, it revealed several trophic interactions occurring at the surface/air interface that were not previously accounted for (Table 1). Ants (Formicidae) and spiders (Pisauridae) were prevalent and exclusive to the diets of *N. atherinoides* feeding in side-channel habitats; while emerging midges (Nematocera) and blackflies (Simuliidae) were indicative of historical and tributary diets respectively. This non-random variation in prevalent diet contributors characterized specific energetic exchanges that occurred between local and adjacent ecosystems.
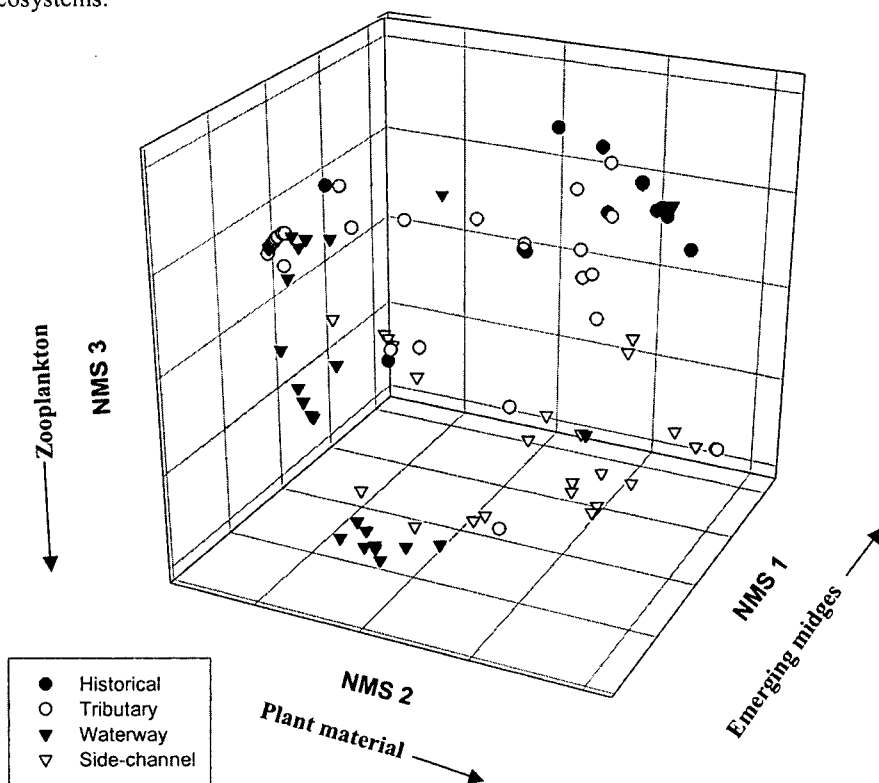

Figure 1. Non-metric multidimensional scaling ordination of *Notropis atherinoides* diets in historical, tributary, waterway and side-channel samples. Variance accounted for by the ordination axes was 13% (NMS 1), 17% (NMS 2) and 20% (NMS 3).

DISUSSION

Some caution is warranted in interpreting the results of the NMS here. First, the Monte Carlo randomization resulted in multiple empty sample units due to a large number of zero states present within the observed data matrix, and this prevented statistical interpretation regarding the non-randomness of the axes extracted by the NMS procedure. Further, mean final stress for the three dimensional solution was 21.86. At this stress level, distances separating *N. atherinoides* individuals on the NMS plot may not accurately reflect separation present within the original matrix (Clarke 1993).

West et al. (2003) reported a similar stress value (i.e., 20.0) for their NMS ordination of gut content data. Large samples sizes may increase stress values, and the

many items present within the gut of some individuals will not be consumed at all by others, leading to a large number of zeros in the data matrix that can prevent Monte Carlo analysis of the NMS solution. These problems may prove common for this application of NMS.

There currently is no consensus regarding a general impact of data transformations and/or relativizations on stress values, likely due to the large variety of these manipulations available to the investigator (Bruce McCune, Oregon State University Department of Botany and Plant Pathology, pers. comm.). We found data manipulations to be useful here as they allowed the incorporation of diet items whose contributions were measured at different scales and they potentially highlighted patterns present in the consumption of less prominent diet items.

Despite potential limitations, NMS ordination provided graphic representation of reasonable ecological gradients both here and for West et al. (2003). For example, it is reasonable that *N. atherinoides* occurring in the relatively lentic waterway will consume greater amounts of zooplankton relative to those feeding under lotic conditions. Complementary analyses are needed to aid in the interpretation of these results and potentially yield greater insight.

Three prominent and complementary patterns emerged when results from our analyses were viewed collectively. First, the diet of *N. atherinoides* feeding within the modified waterway is most strongly separated from those occurring under the historical, unaltered conditions. Individuals within tributaries are most likely to feed differently from one another. Lastly, terrestrial and emerging invertebrates were diet indicators for all individuals except for those occurring in the waterway suggesting, that trophic interactions involving adjacent habitats are less prevalent for *N. atherinoides* in the waterway.

A full discussion concerning possible underlying mechanisms for these patterns was not our purpose here. Rather we emphasize how discernable and biologically relevant patterns can be extracted from copious gut-content data that can exhibit
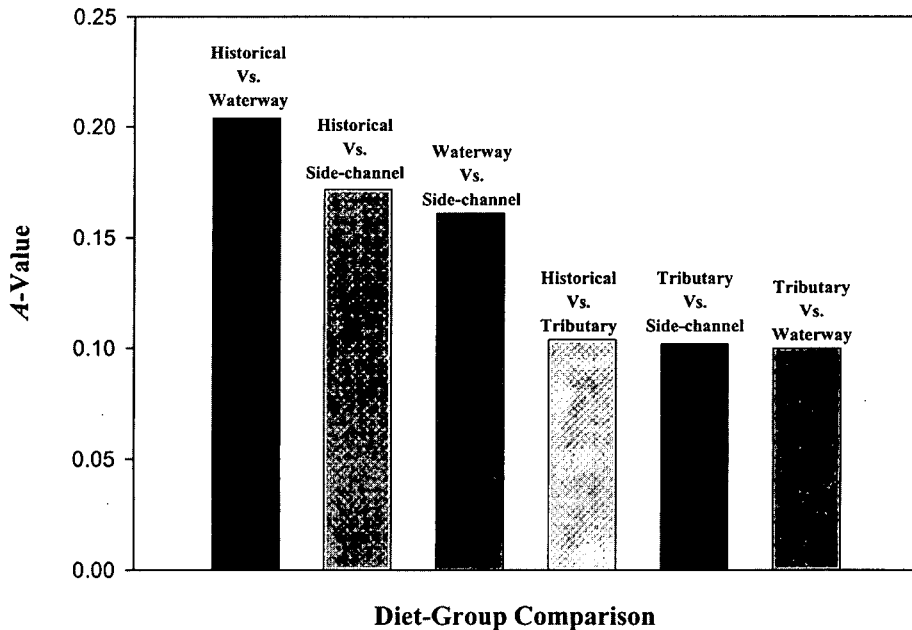

Diet-Group Comparison

Figure 2. Relative within-group diet homogeneity (*A*) for each pair-wise comparison of diet groups.

suboptimal distributional qualities. These analyses proved insightful when comparing the diet of a single species pre- and post-modification of a river system and in delineating current spatial variability in the diet. We suggest that these analyses also may be useful in describing such niche-shifts corresponding to specific ontogenetic stages in a species. Further, it would be interesting to examine their use in describing dietary shifts for whole species assemblages viewed collectively.

Our application of these analyses has focused on patterns of consumption and emphasizes taxonomic linkages. Insight into selective feeding under various conditions was not possible here because data describing the abundance and distribution of diet contributors were not present. When available, these data can be related to those garnered from the examination of gut contents (e.g., Saint-Jaques et al. 2000).

ISA can be used to describe spatial and temporal shifts in diet as described here, and also similar shifts in community composition (e.g., Taylor et al. *in press*). The degree of concordance between diet and community indicators could then be used to discuss the relationship between community structure and inter-specific interactions. For example, a species that is frequently a diet indicator while an infrequent community indicator, may have a relatively high "community importance" in the sense of Power et al. (1996) because the species' community involvement is greater than what would be predicted from its abundance.

Further work is necessary when describing variation in the importance to production of diet items identified through analysis. We suggest that the "spatial tracking" methodology proposed by Melville and Connolly (2003) would be complementary here. Their protocol examined spatial correlations between the isotopic signature of a fish species and that of a food category to suggest the food category's importance with regards to assimilation. In conjunction, the relative importance to production of various diet items can be examined with isotopes using probability modeling (Phillips and Gregg 2003), which calculates feasible combinations of resources that can result in the isotopic signature observed for a consumer of interest.

We hope that the example provided here will draw interest to historical collections housed at museums that characterize past fish and amphibian assemblages. Gut contents extracted from preserved specimens and treated to the methodology we have presented can reveal temporal and spatial dietary shifts, and limited stable isotope analyses may also be possible with these same specimens (Vander Zanden et al. 2003). There is promising potential for community-wide trophic insights, especially when considering trophic linkages before and after major anthropogenic alteration of a system.

Table 1. Results from indicator species analysis. The diet indicated is given along with the associated indicator value for the respective diet item. P values represent the proportion of randomized trials with indicator value equal to or exceeding the observed indicator value.

Diet item	Diet indicated	Indicator value	P value
Daphnidae	Waterway	53.0	0.001
Bosminidae	Waterway	59.4	0.001
Chydoridae	Waterway	25.0	0.001
Adult Nematocera	Historical	40.9	0.001
Adult Simuliidae	Tributary	17.2	0.006
Formicidae	Side-channel	12.0	0.038
Pisauridae	Side-channel	11.2	0.044
Plant material	Side-channel	48.6	0.001

LITERATURE CITED

Altig R., M.R. Whiles, and C.L. Taylor. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. Freshwater Biology 52:386-395.

Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. Annual Review of Ecology and Systematics 16:39-61.

Bond, C.E. 1996. Biology of Fishes. Saunders College Publishing, New York.

Boschung, H. 1989. Atlas of fishes of the upper Tombigbee River drainage, Alabama-Mississippi. Southeastern Fishes Council Proceedings 19:1-104.

Bowen, S.H. 1996. Quantitative description of the diet. Pages 513-532 *in*: Murphy, B.R. and D.W. Willis (eds.), Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117-143.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible assymetrical approach. Ecological Monographs 67:345-366.

Forbes, S.A. 1887. The lake as a microcosm. Pages 14-27 *in*: Real, L.A. and J.H. Brown (eds.), Foundations of ecology: classic papers with commentaries. The University of Chicago Press, Chicago, Illinois.

Fortin, M.J. and J. Gurevitch. 1993. Mantel tests: spatial structure in field experiments. In S.A. Sheiner, and J. Gurevitch (eds.), Design and analysis of ecological field experiments. Chapman and Hall, New York, pp 342-359.

Fry, B. 2006. Stable isotope ecology. Springer, New York.

Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115-129.

Ludwig, J.A. and J.F. Reynolds. 1998. Statistical ecology. John Wiley and Sons, Inc., New York.

Mather, P.M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley and Sons, Inc., London.

McCune, B. and J.B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Glenden Beach, Oregon.

Melville, A.J. and R.M. Connolly. 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136:499-507.

Michener, R.H. and D.M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. Pages 38-157 *in*: Latjtha, K. and R.H. Michener (eds.), Blackwell, Oxford.

Mielke, P.W., Jr. 1984. Meteorological applications of permutation: techniques based on distance functions. Pages 813-830 *in*: Krishnaiah, P.R. and P.K. Sen (eds.), Handbook of Statistics, Volume 4. Elsevier Science Publishers, New York.

Mielke, P.W., Jr. and K.J. Berry. 2001. Permutation methods: a distance function approach. Springer Series in Statistics, Berlin.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69:89-107.

Noy-Meir, I. and R.H. Whittaker. 1977. Continuous multivariate methods in community analysis: Some problems and developments. Vegetatio 33:79-98.

Phillips, D.L. and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269

Power M.E., D. Tilman, J.A. Estes, A. Menge, W.J. Bond, L.S. Mills, G. Daily, J.C. Castillo, J. Lunchenco, and R.T. Paine. 1996. Challenges in the quest for keystones. BioScience 46:609-620.

Roberts, M.E., C.S Schwedler, and C.M. Taylor. 2007. Dietary shifts in the crystal darter (*Crystallaria asprella*) after large-scale river fragmentation. Ecology of Freshwater Fish 16:250-256.

Ross, S.T. 2001. Inland fishes of Mississippi. University Press of Mississippi, Jackson, MS.

Smith, E.P. 1998. Randomization methods and the analysis of multivariate ecological data. Environmetrics 9:37-51.

Taylor, C.M., D.S. Millican, M.E. Roberts, and W.T. Slack. *In press.* Long-term change to fish assemblages after extensive ecosystem fragmentation by the Tennessee-Tombigbee Waterway in Mississippi. Ecography.

Vander Zanden, M.J., S. Chadra, B.C. Allen, J.E. Reuter, and C.R. Goldman. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6:274-288.

West JM, Williams GD, Madon SP, Zedler JB (2003) Integrating spatial and temporal variability into the analysis of fish food web linkages in Tijuana Estuary. Environmental Biology of Fishes 67:297-309.