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Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage

Michael E. Douglas and William J. Matthews

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To test the hypothesis that morphometric data serve as an index of assemblage structure or niche width, 17 fish species (across 8 genera and five families) from the Roanoke River (VA, USA) were evaluated on the following characters: (a) species-occurrence across 12 microhabitat measures; (b) percent occurrence of 13 food items in gut analyses; and (c) 34 head, fin, and body measurements. Ecological data were arcsine transformed, while morphological data were converted first into common logarithms, then into canonical variate scores and scores from a sheared principal components analysis. A taxonomic matrix based on accepted phylogenetic relationships amongst species of the assemblage was also constructed. Microhabitat, trophic, morphological, and taxonomic matrices were then compared against one another using pair-wise Mantel tests, matrix correlation analyses, and three-way Mantel tests. In analyses across families, two-way Mantel tests revealed that taxonomy and body shape (based on sheared principal component scores) were each significantly related to one another, and to the trophic matrix. Yet, three-way Mantel comparisons indicated that body shapes of constituent species were significantly correlated only with taxonomy, and not with diet. To circumvent the confounding effects of taxonomy, the largest family in the study (Cyprinidae, 8 species represented) was then evaluated separately. The same analyses were performed as before, using trophic, microhabitat, and morphological matrices adjusted for numbers of species. In these analyses, morphology (represented by canonical variate and sheared principal component scores) was significantly related to the microhabitat matrix, and to no others. Previous field studies have indicated that cyprinids segregate along habitat rather than trophic dimensions. Ecomorphological analyses thus appear to be a valid assay for structure within fish assemblages only when limited to within-family comparisons (where the effects of history appear less significant). When many different families are involved in the analysis, historical influences predominate.

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The idea of pervasive congruence between morphology and ecology has long intrigued ecologists (see Hubbs 1941, Van Valen 1966, Hespeneide 1973). Longevity and intuitive appeal have shifted this idea from unsubstantiated hypothesis to accepted truism. The mere consistency of the ecomorphological hypothesis with evolutionary theory became the primary criterion for its acceptance, and the transcendent human desire to tell (and to believe) a good story provided ample motiva-

tion. (See Gould 1980, for another application). Aside from intuitive appeal, the most obvious reason for persistence of the ecomorphological hypothesis is stability of the morphological phenotype when compared to other character types. For example, the phenotype of an individual is largely unresponsive to fluctuating environmental conditions (but see Cowl and Covich 1990). This stands in contrast to behavioral and physiological characters which not only respond quickly to local con-

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Table 1. Categories for current speed, substrate size, water depth, and position in water column which compose the microhabitat matrix.

Current (cm s ⁻¹)	Substrate (cm)	Depth (cm)	Water column
0–25	Sand+<5	0–35	Benthic
26–75	6–18	36–75	Non-benthic
>76	19–33	>76	
	Solid		

ditions, but fluctuate greatly during an individual's lifespan. In addition, the phenotype is easily quantified, and historical (e.g. museum) collections can be employed to augment or replicate samples in space and time. (See, for example, Rutherford et al. 1987). Strengths, weaknesses, and methodology of the ecomorphological approach are further discussed by Ricklefs and Travis (1980), and Douglas (1987).

Ichthyologists have been instrumental in pursuing the relationship between phenotypic form and ecological function (Harris 1953, Nursall 1958, Alexander 1967, Aleev 1969, Ovchinnikov 1971). Trophic structures of fish are congruent with observed diets (e.g. Keast and Webb 1966, Beumer 1977, Chao and Musick 1977, Werner 1977, Yoshiyama 1980, Matthews et al. 1982), and body forms of fishes agree in general with observed microhabitat use (Hubbs 1941, Mendelson 1975, Gatz 1979a, b, Baker and Ross 1981, Felley 1984, Felley and Felley 1987, Gorman 1987). Similar relationships have been documented for other vertebrate groups. As a result, some investigators (e.g. Maiorana 1978, Ricklefs and Travis 1980) have argued that ecomorphology is a powerful tool for community-level analyses. Others (e.g. Wiens and Rotenberry 1980) have instead found little correlation between morphology and ecology, which in turn casts doubt on the ecomorphological approach as it has typically been used.

We agree with many of the above researchers that the oft-assumed relationship between phenotype and environment requires critical evaluation before morphological characteristics can be accepted as an accurate index to niche relationships, or as a barometer indicating structure in assemblages of organisms. Few studies to date have attempted to forge this link rigorously. Most rely instead upon subjective assessments and upon a growing literature of univariate and/or descriptive studies (as above). Our investigation, however, applies powerful and versatile matrix comparisons to statistically evaluate an hypothesis of pervasive congruence between phenotype and environment. This is accomplished by comparing morphological, trophic, microhabitat, and historical relationships first within an assemblage of 17 fish species that span five families, and then among 8 species of a single family (Cyprinidae), which coexist within the upper Roanoke River drainage of Virginia.

Methods

Study area

From April to November 1978, a total of 65 fish collections were made at 11 fixed locations in the upper Roanoke River drainage of Roanoke and Montgomery counties, Virginia, USA. The watershed and collecting sites are described in Matthews et al. (1982), Surat et al. (1982), and Matthews (1986, 1990) (also see Jenkins and Freeman 1972). Collecting sites ranged from headwater brooks to the fifth order Roanoke River mainstream. The headwaters drain steep slopes of the Blue Ridge and Ridge and Valley physiographic provinces, and thus typically have high gradients, a shading forest canopy, and riffle-pool zonation over bottoms of gravel, rubble, shale, or bedrock. Mainstreams have lower gradients with large, swift riffles, occasional backwater pools, and long stretches of rather uniform channel. Collections were dominated numerically by minnows (Cyprinidae), darters (Percidae), suckers (Catostomidae), madtom catfishes (Ictaluridae), and sculpins (Cottidae). Centrarchids were taken only rarely in our samples, and hence were excluded from analyses. All study species were collected at all mainstream sites, with the greater majority collected from small headwaters as well (i.e. within 1 km of the mainstream). Matthews (1986: Table 2) and Surat et al. (1982: Fig. 1) further clarify distribution of study species within the watershed.

Microhabitat data

At each collecting site, approximately one hour was spent seining each available discrete microhabitat (e.g. slow and fast riffles, deep and shallow pools, main channel, etc.). Within each microhabitat, three environmental factors were evaluated: current speed (recorded with a General Oceanics Model 2030-R current meter), predominant substrate size (estimated to the nearest cm), and average water depth (estimated to the nearest 10 cm). These three environmental factors can strongly influence microhabitat distributions of freshwater fishes (see Bain et al. 1988, and references therein). Microhabitat use by each study species thus consisted of percent occurrence within the microhabitat categories of Table 1. These data were first transformed into arcsine values, then into measures of dissimilarity (taxonomic distances, Sneath and Sokal 1973) between all 136 possible pairs of fish species by using NT-SYS (Numerical Taxonomic System of Multivariate Statistical Programs, Rohlf et al. 1972). Taxonomic distances were used simply to produce coefficients between every species-pair and to place all matrices within a similar analytical framework. Distances are non-negative and low values indicate similarity. Distance values for the microhabitat matrix were then clustered with the unweighted pair-

Table 2. Thirteen food categories which comprise the trophic matrix.

Rough material	Aquatic adults	Low motility forms
Plant material	Larval chironomids	Decapods
Aquatic larvae	Hellgrammites	Fish eggs
Aquatic pupae	Terrestrial insects	Fish
	Worms	

group method using arithmetic averages (e.g. UPGMA, Sneath and Sokal 1973), and summarized in a phenogram. A matrix correlation coefficient (r , Sokal and Rohlf 1962) was computed as a measure of distortion between distance matrix and phenogram (see Schnell et al. 1978 for an application of this technique).

Trophic data

Stomach contents of 73–120 individuals were evaluated for six of the 17 species (Matthews et al. 1982, Surat et al. 1982). For the other 11 species, stomach contents were evaluated for 20 individuals each, collected at numerous localities within the study area during the warm months. While this sample does not permit a detailed statement of variance in foods used by a species across seasons and localities, it does provide a picture of the range of foods ingested, and agrees with sample sizes used to compare diets among birds (Wiens and Rotenberry 1980), rodents (M'Closkey 1980), lizards (Pianka and Pianka 1976, Pianka and Huey 1978), and fish (Ross 1977, 1978, Baker-Dittus 1978, Yoshiyama 1980). These data also agree with previously published accounts of food use by the study species (e.g. Meredith and Schwartz 1959, Schwartz and Dutcher 1962, Flemer and Woolcott 1966, Hobson 1979). The percent occurrence of the 13 food items (listed in Table 2) were transformed into arcsine values, then into pair-wise taxonomic distances. Phenograms and matrix correlations were also produced for these data as before.

Morphological data

Thirty-four morphological characters (see Appendix), were measured on ten individuals of each species collected during our field studies. Computational difficulties that relate to within-species allometric growth were minimized by restricting analyses to adult individuals only (see Schnell et al. 1985b). All morphological measurements were completed by one individual (WJM) within two years of collection. Choice of characters reflected ecological importance (e.g. characters describe body form, placement or size of fins, position of eye, size of trophic apparatus, etc.). In this regard,

numerous characters measured by Gatz (1979a, b), and Douglas and Avise (1982), were used. Characters that were either strongly diagnostic or which occurred in only a few species (e.g. numbers or shape of pharyngeal teeth in cyprinids) were excluded. The common logs of these data were converted into taxonomic distances which represented our first morphological data set.

Two additional morphological matrices were created by converting raw data to a different reference system. First, size-corrected data were produced through the use of sheared principal component analysis (Humphries et al. 1981, Bookstein et al. 1985, Rohlf and Bookstein 1987). This multivariate technique derives a linear combination of variables that quantifies shape differences among groups independent of size. This is accomplished by extracting size (= component one) from subsequent components through the use of sheared coefficients calculated from regression of overall size onto principal components centered by group. The general size factor is estimated by the principal axis of the within-group covariance matrix of log-transformed data. Residuals from regression of overall size onto the transformed axes approximate a shape-discriminating factor uncorrelated with general size within groups. Principal component scores, calculated from sheared principal component axes 2–4, thus formed our second morphological matrix. These were produced from an algorithm written by L.M. Marcus, (modified by Rohlf and Bookstein 1987), and implemented by MED.

Loadings from the first four axes of a canonical variate analysis (CVA) were also used, as CVA makes a multivariate "allowance" for the overall size of grouped specimens that other multivariate techniques (such as principal components analysis) do not. The statistical reasoning for this statement is explained lucidly by Albrecht (1978), and Oxnard (1984). The geometry of canonical variate analysis is reviewed by Campbell and Atchley (1981), while the relationship of canonical axes to niche hyperspace is presented by Carnes and Slade (1982). Although PCA and CVA are both data summarization techniques, CVA differs markedly from PCA in that it weights between-group differences using the within-group dispersion. Also, the first axis of CVA is not size-related, as it is in PCA. Canonical variate scores for our morphological data were generated by BMDP-7M of the BioMedical Computer Programs library (Dixon 1983). The matrix of canonical variate scores, as well as the sheared matrix derived above, were then converted into matrices of taxonomic distance between species-pairs, using NT-SYS.

Another multivariate technique frequently used in ecomorphological studies is canonical correlation analysis (Calhoun and Jameson 1970, Karr and James 1975, reviewed by Smith 1981). Some researchers would argue that canonical correlation analysis is the only multivariate method applicable for the evaluation of morphological and ecological data sets. However, it could not

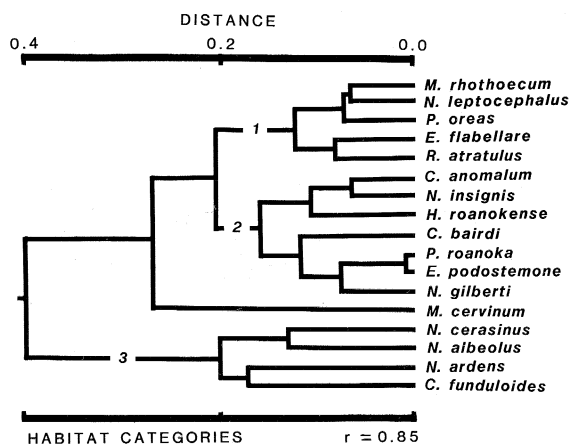


Fig. 1. UPGMA phenogram showing relationships between the 17 fish species based on microhabitat. The matrix correlation (r) is indicated.

be applied in our investigation because our covariance matrices were not full-rank (e.g. they contained more variables than species). This is frequently the case with most community-level studies.

Taxonomic model

To test if assemblage-wide morphological distance matrices were statistically congruent with accepted phylogenetic classification, a taxonomic model was constructed in the following manner: a value of 1 was assigned for congeneric species-pairs, a value of 2 was given to species-pairs in different genera but within the same family, species-pairs from different families but the same order were scored 3, and species-pairs from different orders were scored as 4. The resulting matrix thus reflects known taxonomic relationships among our study species (following Nelson 1976).

Statistical comparison of data matrices

Mantel (1967) devised a generalized, non-parametric regression approach to matrix comparisons, in which the sum of cross-products of analogous cells of two matrices are compared against an expected value calculated on the null hypothesis of random permutations between rows/columns of the second matrix (the computation is actually the inner product of each permutation with the first matrix). Because Mantel's procedure evaluates all possible permutations of the rows and columns of the second matrix, it employs a generalized permutational distribution to assess the statistical significance of the resulting congruence value (see Jackson and Somers 1989). Because the test is non-parametric, distributional abnormalities associated with data collected from different sources (e.g. ecological, morph-

ological, geographical, etc.) are avoided. In addition, potential problems with comparing categorical vs continuous data (in our case, taxonomy vs morphology or ecology) are negated as well. Sokal (1979) brought Mantel's test to the attention of systematists, and suggested applications in geographic variation analysis, several of which were performed by Schnell et al. (1986). Other uses of the test (with examples) can be found in Douglas and Endler (1982), Schnell et al. (1985a), and Manly (1985).

In this paper, pair-wise Mantel tests were used to evaluate two null hypotheses which assume either no covariation or significant negative covariation when the morphologies of our study fish are compared against observed habitat requirements and trophic relationships. As in previous work (e.g. Douglas and Endler 1982), the Bonferroni technique (Harris 1975:96–101) was used to assign significance levels and to establish a probability level for making a family Type 1 error (e.g. identifying a matrix comparison as significant when it is not). Under the conservative Bonferroni technique, the probability level for our tests would be $(0.05/n)$, where n = the number of matrix comparisons. A one-tailed test is appropriate because positive covariation between two test matrices would agree with untested predictions from the literature which suggest that morphology is, in some way, positively associated with ecology (e.g. Van Valen 1966, Hespeneheide 1973).

Smouse et al. (1986) modified and extended the methodology so that three matrices could be contrasted simultaneously. This allows correlations and partial correlations to be generated between matrices, which are then used to calculate coefficients of multiple determination (as in Smouse et al. 1986). Three-way Mantel comparisons were used in this study to extend those two-way tests in which significant results were found between a given matrix and two or more "response" matrices. Rows and columns of test matrices were permuted 10 000 times for each evaluation (as per Jackson and Somers 1989).

Results

Species comparisons

The microhabitat phenogram (Fig. 1) reveals three large species-clusters, the first of which (cluster 1, Fig. 1) can be subdivided into two groups: the upper consists of forms often found in slower current and shallower water, and which feed on the bottom over a substrate of sand or small rock. The lower group includes two shallow water bottom-dwellers, but differs from the upper in affinity for slow-to-moderate currents over a diversity of substrates.

Cluster 2 of Fig. 1 also is composed of two groups: the upper contains bottom-dwelling fishes that typically occupy relatively shallow waters, moderate currents

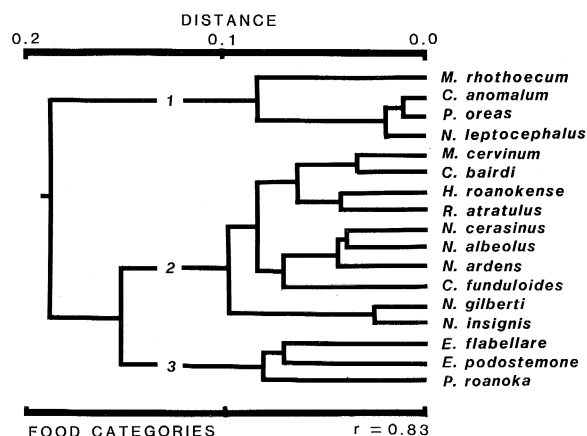


Fig. 2. UPGMA phenogram showing trophic relationships between the 17 fish species based upon an evaluation of ingested foods. Matrix correlation (r) is indicated.

(26–75 cm s^{-1}), and intermediate-sized substrates (diameter = 19–33 cm). The lower group of cluster 2 also links bottom dwellers which occupy moderate currents in shallower water. However, the species of this lower group display a much stronger affinity for more moderate-sized substrate than do those in the upper group. The weak association between the sucker, *Moxostoma cervinum* and species forming clusters 1 and 2 is based upon the sucker's affinity for slow-to-moderate currents, sand-to-moderate-sized substrates, and a completely benthic existence. However, this species differs from those in the first two clusters by occupying relatively deeper water (e.g. > 75 cm).

The third and most deviant cluster in the phenogram (cluster 3, Fig. 1) is composed of four cyprinids which collectively prefer slower currents, deeper waters, and sand-to-small-pebble substrates. These four species split into two distinct groups which differ according to relative positions within the water column (e.g. bottom – *N. cerasinus* and *N. albeolus* vs upper-and-middle – *N. ardens* and *C. funduloides*, respectively).

Trophic phenogram

Three distinct clusters are recognized in the trophic phenogram (Fig. 2). Cluster 1 is the most deviant, depicting a tight group of three cyprinids which feed almost exclusively upon plant material or detritus (with some accumulation of sand as well). The catostomid *M. rathoeum* shows weak affinity with this group, based upon a similar preference for plant material, sand and detritus. However, the sucker ingested proportionally more sand and detritus (as well as a small percentage of chironomid larvae) than did the cyprinids.

Cluster 2 is the largest of the phenogram, and is conveniently subdivided into two groups. The upper is composed of a sucker (*M. cervinum*), a sculpin (*Cottus*

Table 3. Two-way Mantel comparisons between the 17-species matrices of this study. H represents the matrix of sheared principal component scores, while CAN represents scores from a canonical variate analysis. LOG indicates log (base 10)-transformed morphological measurements, while TAX indicates the taxonomic matrix. TROPH and HAB represent trophic and habitat matrices, respectively. Upper triangle contains values for Mantel test, while lower triangle indicates matrix correlations. Statistical significance is demonstrated by asterisk.

	CAN	H	LOG	TAX	TROPH	HAB
CAN	X	5.14*	3.87*	5.08*	0.83	1.14
H	0.77	X	3.72*	6.08*	3.38*	1.44
LOG	0.54	0.46	X	0.48	0.28	0.01
TAX	0.73	0.77	0.48	X	3.35*	1.01
TROPHIC	0.12	0.42	0.28	0.39	X	0.11
HABITAT	0.17	0.18	0.13	0.01	0.01	X

*: $p < 0.0033$.

bairdi), a second sucker (*Hypentelium roanokense*), and a cyprinid (*Rhinichthys atratulus*). The sucker/sculpin pair has a dietary preference for low motility aquatic larvae, plant material, and chironomid larvae; the sucker/cyprinid tandem ingested the same categories of food but in markedly different proportions (plant material being eaten in greatest percentage, followed in descending order by chironomid larvae, sand and detritus, and low motility aquatic larvae). The lower group of cluster 2 is composed of four cyprinids (three *Notropis* and *Clinostomus funduloides*). The shiners (i.e. *Notropis*) fed upon active aquatic larvae, plant material, chironomid larvae, low-motility aquatic larvae, and terrestrial insects (Surat et al. 1982), while *C. funduloides* ingested the same food types but with different preferences (e.g. terrestrial insects, active aquatic larvae, low-motility aquatic larvae and chironomid larvae, in descending order). The two madtom catfish (*Noturus gil-*

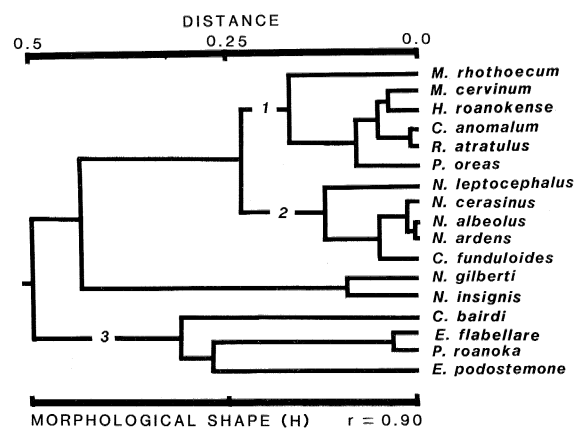


Fig. 3. UPGMA phenogram of relationships between the 17 species of fish based upon size-free body shape (generated using sheared principal components analysis). Matrix correlation (r) is presented.

Table 4. Results of three-way Mantel analyses between body shape, taxonomic, and trophic distance matrices compiled for the 17-species assemblage. Formulations as per Smouse et al. (1986).

Model: Body shape = Taxonomy, Trophic ecology
(Y) = (X1) (X2)

Comparison	Formulation	Correlation	Probability
Shape-Taxonomy	r_{Y1}	0.77	$p < 0.0001$
Shape-Trophic	r_{Y2}	0.42	$p < 0.0004$
Taxonomy-Trophic	r_{12}	0.39	$p < 0.0005$
Shape-Tax(Trophic)	$r_{Y1.2}$	0.76	$p < 0.0001$
Shape-Trophic(Tax)	$r_{Y2.1}$	0.19	$p > 0.07$

berti and *N. insignis*) fed upon low-motility larvae, active aquatic larvae and chironomids (in descending order), and are thus weakly associated with cluster 2. Three darters form cluster 3, and all fed ($> 60\%$) upon chironomid larvae (Matthews et al. 1982). The two *Etheostoma* also ingested more low-motility aquatic larvae, whereas the *Percina* foraged more on active aquatic larvae and aquatic pupae.

Morphological shape phenogram

Based upon results of Table 3, only the UPGMA-phenogram based upon sheared principal component scores is presented. This phenogram (Fig. 3) suggests a strong, overall taxonomic influence within the sheared data (for instance, cluster 2 of Fig. 3 represents the family Cyprinidae). However, on occasion, morphological nearest-neighbors within clusters sometimes cross generic lines such that some species were morphologically closest to species of a different genus. For example, in cluster 1, the sucker *M. rhothoecum* is morphologically separated from other catostomids (*M. cervinum* and *H. roanokense*) by the intervention of three cyprinids, two of which are morphologically quite similar, the third less so.

Cluster 2 is formed by five cyprinids, with the shiner genus *Notropis* forming the morphologically most similar core of the cluster, followed by *C. funduloides* and the morphologically most divergent *Nocomis leptoccephalus*. Clusters 1 and 2 show similarities with the madtom catfishes (*N. gilberti* and *N. insignis*), which diverge from the main stem at a relatively greater distance.

The most divergent cluster of the phenogram contains three darters and the cottid. In this cluster, *E. flabellare* is morphologically closer to *P. roanoka* than to its congener, *E. podostemone*. Based upon size-free shape residuals, the cottid shows close affinities with the darter group. However, all four are bottom-dwelling fish with morphologies that are similar amongst themselves, yet deviate greatly from those expressed by the majority of assemblage members (as evidenced by the early divergence of cluster 3 from the main stem of the phenogram). Distortion is minimal between the phenogram

and its distance matrix, as indicated by the matrix correlation value of $r = 0.90$.

Covariation between assemblage matrices

Two-way Mantel comparisons between microhabitat and trophic matrices were non-significant, as were microhabitat and morphological comparisons. The only congruent matrix comparisons were those between trophic, taxonomic and morphological shape (Table 3). To unravel the interrelationships between trophic ecology, taxonomy, and body shape, a three-way Mantel analysis was then performed. The resulting correlations and partial correlations (Table 4) indicate that body shape has both taxonomic and trophic components (e.g. both X-matrices are useful predictors of the Y-matrix). However, body shape is more highly correlated with taxonomy ($r_{Y1} = 0.79$, $p < 0.0001$) than with trophic ecology ($r_{Y2} = 0.42$, $p < 0.0004$). The partial correlation of body shape and taxonomy is significant ($r_{Y1.2} = 0.76$, $p < 0.0001$), whereas that of body shape and diet is not ($r_{Y2.1} = 0.19$, $p > 0.07$). Results from the partial correlation analysis (Table 4) can be more clearly understood through an evaluation of coefficients of multiple determination. Once having fit taxonomy to the model (Table 4), there was virtually nothing to be gained by adding trophic ecology as R^2 (the coefficient of multiple determination) was only increased from 0.628 to 0.644. On the other hand, once having fit trophic ecology to the model ($R^2 = 0.176$), considerably more information was obtainable by then adding taxonomic relationships ($R^2 = 0.644$). Covariation between matrices is presented in Fig. 4.

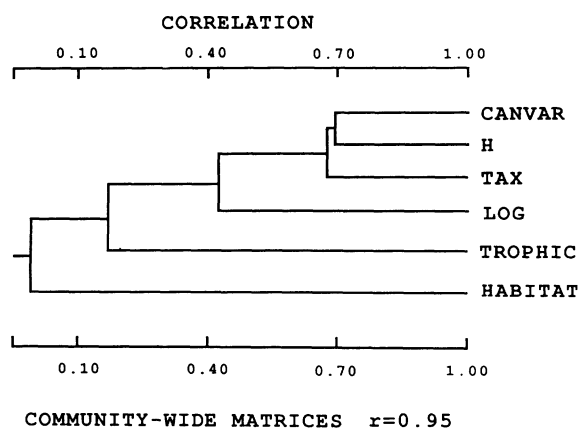


Fig. 4. UPGMA phenogram showing similarities among microhabitat, trophic and morphological data matrices for the 17 species community of fishes. Matrix correlation (r) is depicted.

Table 5. Two-way Mantel comparisons between the 5 Cyprinid matrices of this study. Matrix descriptions as in Table 3. Statistical significance is demonstrated by asterisk.

	CAN	H	LOG	TROPH	HAB
CAN	X	4.11*	0.52	1.93	3.59*
H	0.81	X	1.21	2.16	3.52*
LOG	0.10	0.22	X	0.51	0.30
TROPHIC	0.39	0.43	0.09	X	2.74
HABITAT	0.71	0.69	0.06	0.55	X

*: $p < 0.005$.

Covariation between cyprinid matrices

Canonical variate (CV) and shape (H) matrices for the 8 minnow species were each significantly related to the microhabitat matrix (Table 5). However, comparisons between morphological and trophic matrices were non-significant. Body shape (H), trophic, and microhabitat phenograms are presented for the Cyprinidae in Fig. 5. Covariance between various cyprinid data sets is presented in Fig. 6, illustrating the overall close link between microhabitat and morphology within this group.

Discussion

Can morphological attributes of an organism predict ecological attributes (e.g. where it dwells and what it eats)? This question (whether morphological “space” maps onto ecological “space”, Strauss 1987) tests an important aspect of ecomorphology, for if it can be rejected, then structure in natural assemblages would be constrained not by physical adaptations of organisms for specific niches, but by a different (possibly unspecified) organizing principle. Alternatively, structure in natural assemblages may only be perceived by researchers, and may represent nothing more than imposition of human orderliness onto a stochastic assemblage of organisms. In this study, we have employed multivariate morphometric methods and techniques from geographic variation analysis to address the question of morphological links to ecological function. Our analyses do not address variance in ecological or morphological data, nor the manner in which morphology may lead to either narrow or broad resource use. Our conclusions are multi-faceted, but speak in general for an historical rather than a contemporary perspective of organization in fish assemblages beyond the family level. We note, for instance, that the shape matrix for our larger (17 species) assemblage is congruent with the trophic matrix (Table 3, Fig. 4). Although this result supports previous predictions (Wiens 1984: 441) that food use and body shape will covary positively within an assemblage of organisms, it generates little excitement on our part. Instead, we find more interesting the fact that our phe-

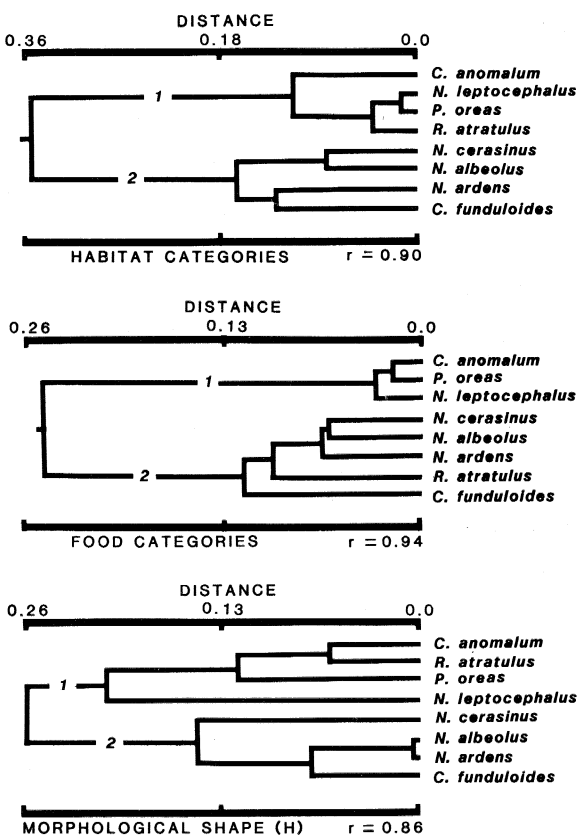


Fig. 5. UPGMA phenograms depicting relationships between the 8 cyprinid species based on (top) microhabitat, (middle) ingested foods, and (bottom) size-free body shape (generated using sheared principal components analysis). Matrix correlations (r) are depicted for each phenogram.

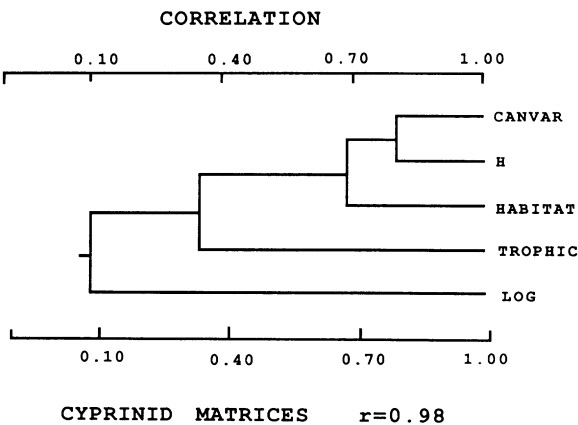


Fig. 6. UPGMA phenogram depicting similarities among microhabitat, trophic, and morphological data matrices for the 8 species of cyprinid fishes in the analysis. The matrix correlation (r) is also presented.

notypic characters, selected on the basis of ecological rather than diagnostic (e.g. taxonomic) utility, still placed most species into taxonomically-aligned groups, particularly at the family level (Fig. 3). Most fish taxa (including those dealt with herein) were originally described on the basis of morphology, and these relationships (rather than ecological ones) seem to dominate our results, even though a serious attempt was made to keep morphological data unbiased. It may thus be that morphological data are inappropriate to serve as an indicator of overall structure in assemblages. In fact, an element of circularity may be involved with the use of morphological characters in ecological analyses. If morphology was originally used to produce taxonomy, it would indeed be surprising if morphological evaluation of ecological relationships did not produce taxonomic results. The philosophical implications of this point are recognized but not pursued in this paper. They are also addressed in an evolutionary context by Douglas and Avise (1982).

Indeed, could the question of ecological segregation of fishes along a trophic axis be nothing more than an ordinary exercise in alpha-taxonomy? Some researchers (for example, James et al. 1984) have alluded to this premise by arguing that species in an assemblage respond to resources on the basis of their own individual evolutionary histories (see also Eberling and Laur 1986, Martin 1988). In this sense, the assemblage would simply represent a loose aggregation of species exploiting similar resources. Perceived patterns of resource utilization would then be due not to biological processes, but to historical artifact. The influence of history in the overall structuring of a stream fish assemblage may, in fact, be so great that phylogenetic relationships between component species must become an hypothesis against which other patterns are tested. The hypothesis of "historical origin" has, in fact, become a significant component of many recent comparative studies: functional morphology (Lauder 1981, 1982), life history (Stearns 1983, 1984), ecological associations (Mitter and Brooks 1983), behavior (Dobson 1985), species associations (Mayden 1987). The historical origin hypothesis is tested by contrasting ecological or life-historical characteristics of study species against a defined phylogeny. If the distribution of characteristics among species is inconsistent with the accepted phylogeny, then several (independent) evolutionary events would be required to explain the distribution of the characteristics. It would thus be unlikely, given this situation, that historical origin has been influential in the distribution of the characteristics studied.

Many ecomorphological studies have actually demonstrated (frequently in an indirect manner) just such an association between morphology, ecology, and taxonomy. For example, in a community study similar in format to our own, Gatz (1979a) grouped 33 fish species on the basis of an ecomorphological analysis. The first axis produced by his factor analysis (Gatz 1979a: Fig.

1), accounted for 31% of the total variance and grouped all cyprinids at the negative end of the axis while scattering all percids toward the positive end of the axis. Centrarchids fell between zero and +1, while the catostomids were in the lower portion of the axis. Although Gatz interpreted scores on his first axis as differences in feeding strategy between "sit-and-wait", biting predators (with high scores on factor 1), and cruising, suction predators (with low scores on factor 1), he was also cognizant of factor 1's strong taxonomic bias at the family level (Gatz 1979a:102). We strongly suspect that other studies of an ecomorphological nature would provide similar (yet untested) relationships between the taxonomic status of organisms and their ecologies.

If this is indeed so, then the following question must be posed: does the strong influence of phylogeny within the trophic relationships of an assemblage negate the value of an ecomorphological analysis in determining the overall structure of an assemblage? We would argue "yes." The morphology of an organism is an inextricable mix of homologous similarities retained by history (and used in the formation of traditional classifications), and analogous similarities evolved independently through convergence (Gould 1986, Wagner 1989). If patterns of morphological variability in an assemblage are dictated by homology, then genealogy fills niches and competition should be restricted to recently evolved forms in the same genus. However, if convergent morphology is important in dictating the structure of fish assemblages, then competition should be the constraining factor within assemblages, for many separate lineages are being driven by environmental forces towards similar ecological niches. Strauss (1987), in an analysis of morphotypes in North and South American fish assemblages, found that consistency of form (or lack of it) among different fish assemblages is a result of phylogeny rather than convergence. Hence, Strauss concluded that ability to predict patterns of morphological variation in one community from patterns observed in another is limited by the degree to which species share homologous structures. Our analyses also suggest that history and homology, rather than environment and convergence, seemingly dictate at least a substantial portion of structure and resource use within assemblages as well. It thus appears that taxonomy and trophic ecology are inextricably intertwined, and that resource use in the assemblage reflects phylogenetic artifact. Segregation of fishes along a trophic axis simply echoes taxonomic status of component species. Indeed, 3-way Mantel analyses (Table 4) demonstrate that body shape-taxonomy relationships within our fish assemblage completely overshadow those between body shape and trophic ecology. [The partial correlation between body shape and taxonomy (e.g. the correlation between these two matrices given the association between body shape and trophic ecology) is virtually as strong as the correlation solely between body shape and taxonomy ($r_{Y1.2} = 0.76$ vs $r_{Y1} = 0.79$, Table 4)]. Con-

versely, the partial correlation between body shape and trophic ecology (e.g. that correlation given the association between body shape and taxonomy), is non-significant ($r_{Y2.1} = 0.19$, Table 4). One could thus argue that trophic ecology of individual species within the assemblage has little significance when removed from a taxonomic framework. In fact, the assemblage's trophic ecology is itself taxonomically structured ($r_{12} = 0.39$, $p < 0.0005$, Table 4).

These results should not be all that surprising. Much of what a fish does in an assemblage seems to be constrained phylogenetically. (By this, we mean that the phenotypes of these fishes, as manifested by their body shapes, prevents them from evolving along particular pathways. Since, by our analyses, body shapes are statistically congruent with taxonomic relationships, we simply state in shorthand that the fishes are "phylogenetically constrained". An example of phylogenetic constraint would be limitations imposed by mouth size, buccal architecture, fin lengths, and peduncle depth upon sizes and types of prey ingested. As used in this paper, "phylogenetic constraint" is not a mechanistic term, but rather an indication of process. Our argument is simply that phenotypes of fishes act as a fundamental constraint upon their ecologies. These same phenotypes are also statistically congruent with taxonomic classification). While our tests are only within a single assemblage (rather than between assemblages), the importance of phylogenetic constraint is nevertheless apparent. At the family level, phylogeny seemingly dictates morphology which, in turn, canalizes ecology. The result is that catfish, darters, and suckers, for example, display stereotypic morphologies, and perform largely in a categorical manner. Interrelationships between function (= body shape), diet, and taxonomic status are thus predictable.

Indeed, if the relationship between diet, body shape, and taxonomy is predictive at the community level, then perhaps greatest new information would stem from a more intimate juxtaposition of morphology with ecology, such as within boundaries of distinct families rather than across divergent taxonomic groups. To test this hypothesis, we contrasted morphological and ecological characteristics of species from the largest family in the drainage, the Cyprinidae. In this way, by limiting our scope to 8 species representing a single family, we minimized the potential bias of taxonomy, and focused instead on ecological relations. [In other words, we could ascertain if there is room within families for inter-specific interactions to "fine-tune" structure of assemblages.] Several previous ecomorphological studies have, in fact, been limited in scope to one well-defined taxon (Findley 1973, 1976, Ricklefs and Cox 1977, Smart 1978, Sheldon 1980).

Although our analyses of food use and body shape generally placed cyprinids into two broad groups (Fig. 5b, c), the pattern of covariance was blurred sufficiently to render non-significant the test between morphology

and trophic ecology. However, congruence between cyprinid microhabitat and morphology was clearly apparent (Fig. 5a, c, Table 5, Fig. 6). Schoener (1974) noted that separation of coexisting species along spatial dimensions was the most common attribute of terrestrial communities, with trophic and temporal separation secondary. Schoener suggested, however, that spatial separation may assume less importance among aquatic organisms. Although older studies of fish communities concentrated primarily on dietary differences between species (e.g. Starrett 1950, Keast and Webb 1966), recent investigations in a variety of aquatic habitats reinforce the importance of habitat structure in distribution and coexistence of fishes: lacustrine systems (Werner 1977, Werner et al. 1977), marine environment (Ross 1977), temperate streams (Gorman and Karr 1978), tropical streams (Watson and Balon 1984). Cyprinids, for example, frequently coexist within large multispecific aggregates, and specialize more with respect to microhabitat than to food (Mendelson 1975, Baker and Ross 1981, Surat et al. 1982, Felley 1984, Felley and Felley 1987, Gorman 1987). Our morphological analyses of overall body shape thus predict ecological relationships within Cyprinidae along the niche axis of greatest importance (Table 5, Fig. 6).

Perhaps it is demanding too much from an ecomorphological approach to perform equally well both within and among higher taxonomic categories, or within and among forms that are ecologically very different (such as large predators vs small omnivores). To demonstrate our point, we note that cluster 2 of Fig. 1 (the microhabitat phenogram) is composed of two groups: the upper contains a cyprinid (*C. anomalum*, family Cyprinidae), a madtom catfish (*N. insignis*, family Ictaluridae), and a sucker (*H. roanokense*, family Catostomidae). All are bottom dwellers, preferring relatively shallow waters, moderate currents, and intermediate-sized substrates. The lower group of cluster 2 links two darters (*E. podostemone*, *P. roanoka*, family Percidae) and a madtom (*N. gilberti*, family Ictaluridae) with a cottid (*C. bairdi*, family Cottidae). Again, these are bottom-dwelling species found in shallow waters with moderate currents over moderately-sized substrates. These 7 species span five families; their overall morphologies are obviously quite different, even without our detailed analyses (Fig. 3). Yet, these forms occupy very similar microhabitats through quite different morphological adaptations, using in effect alternate solutions to the same ecological problems.

In closing, we would argue that a mechanistic approach to ecological phenomena (Schoener 1986), in which individual ecological concepts are used as a basis to interpret ecological theory, does indeed provide valid tests for community-level hypotheses. Using this approach, we conclude that, in a broad view, organization of stream fish assemblages has been guided more by common evolutionary history rather than by convergence, and by phylogeny rather than environ-

ment. Adaptations by North American stream fishes appear most possible within distinct morphological constraints imposed by phylogeny at the family level. Competition may be important in structuring stream fish assemblages, but largely within genera and particularly between recently evolved forms. Competition may also be an important factor when fish assemblages are restructured through addition of exotics, or other such non-native forms. Use of ecomorphology as a tool to evaluate structure of assemblages is valid when analyses are restricted in scope (at least for fishes) to comparisons within families. Ecomorphological analyses across families are clearly confounded by phylogenetic history. Furthermore, by employing phylogeny as a null hypothesis against which community-related phenomena are tested, ecology becomes integrated with, rather than estranged from, the historical process.

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Appendix

The following morphological features were included in the analysis (following Hubbs and Lagler 1970, Gatz 1979a, or Douglas and Avise 1982): (1) body depth, (2) body width, (3) tip of snout to maximum depth of body, (4) caudal peduncle length, (5) caudal peduncle width, (6) caudal peduncle depth, (7) head length, (8) tip of snout to occiput, (9) head depth, (10) head width, (11) snout length, (12) interorbital distance, (13) suborbital distance, (14) postorbital distance, (15) eye diameter, (16) distance between nares, (17) height of opened mouth, (18) gape width, (19) upper jaw length, (20) lower jaw length, (21) pre-naris length, (22) pre-dorsal fin length, (23) pre-pectoral fin length, (24) pre-pelvic fin length, (25) pre-anal fin length, (26) pectoral fin length, (27) pelvic fin length, (28) anal fin height, (29) dorsal fin height, (30) vertical span of caudal fin, (31) length of dorsal fin base, (32) length of anal fin base, (33) length of pectoral fin base, (34) length of pelvic fin base.