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MULTIVARIATE IDENTIFICATION OF MORPHOLOGICAL - ENVIRONMENTAL RELATIONSHIPS WITHIN THE CYPRINIDAE (PISCES)

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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MULTIVARIATE IDENTIFICATION OF MORPHOLOGICAL-ENVIRONMENTAL RELATIONSHIPS WITHIN THE CYPRINIDAE (PISCES)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

JAMES D. FELLEY

Norman, Oklahoma

1980

MULTIVARIATE IDENTIFICATION OF MORPHOLOGICAL-ENVIRONMENTAL

RELATIONSHIPS WITHIN THE CYPRINIDAE (PISCES)

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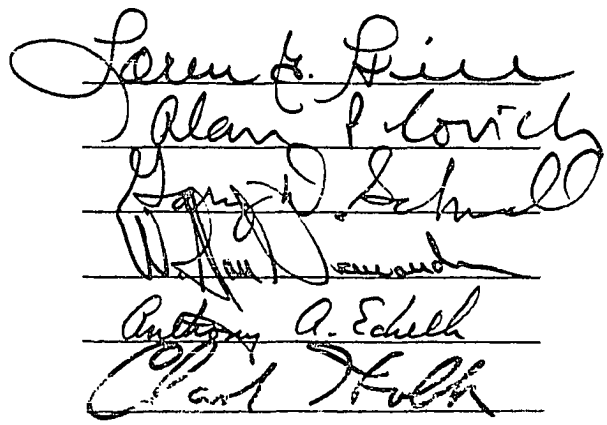

DISSERTATION COMMITTEE

PREFACE

This study is written in the form required by the journal Ecology, of the Ecological Society of America. This study will be submitted to Ecology for publication.

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MULTIVARIATE IDENTIFICATION OF MORPHOLOGICAL-ENVIRONMENTAL RELATIONSHIPS WITHIN THE CYPRINIDAE (PISCES)

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Abstract. A method is presented that allows identification of covariation between sets of environmental preferences and morphological characters for a group of species. Preferences for environmental parameter states are identified and morphological characters measured for species of the taxon in question. A factor analysis procedure is used to group the environmental parameters and morphological characters into covarying sets. Morphological characters grouped with a given environmental parameter are interpreted as evidencing adaptations relating to that parameter. Fishes of the family Cyprinidae were used to evaluate this method. Species of the genus Notropis were collected from 124 localities in Oklahoma. Environmental preferences were assessed for these species and their morphological characters were measured. The

principal components solution, with rotation to simple structure, identified sets of morphological characters related to habitat use (preference for varying amounts of vegetation in the environment, preference for a benthic versus an open-water habit, and amount of detritus and periphyton eaten). These results were expressed in regression equations relating an environmental parameter to the appropriate set of morphological characters. Correlations and rank correlations were calculated between predicted and actual habitat use for a second group of cyprinid species. The results for test species showed that habitat use of individual fish species can be successfully predicted from regression equations based on morphological characters (those identified by the principal components analysis as relating to environmental preferences).

Key words: morphology, habitat use, multivariate, adaptation, Cyprinidae, principal components

INTRODUCTION

It is generally held that morphological adaptations to environment help determine the place of an organism in its ecosystem. This assumption is basic to studies that determine niche dimensions from morphological differences of species in the community (Findley 1973, Hespenheide 1975, Gatz 1979a). Morphological adaptations to environment, though assumed to exist, are not well understood for many groups of organisms.

The aim of this study was to develop a method whereby morphological features for a number of species may be identified as adaptations associated with certain environmental parameters. The method may be summarized as follows: Morphological characters and environmental preferences are measured for the set of species under consideration. A factor analytic procedure (principal components analysis, factor analysis, or image analysis; Mulaik 1972) is used to group the environmental and morphological variables into sets which are assumed to represent functional relationships among variables. Associations among groups of variables identified by factor analysis may be tested by regression techniques (Nabholtz and Richardson 1975).

Environmental-morphological relationships in fishes are relatively well understood (Alexander 1967, Aleev 1969, Gosline 1971, Gatz 1979b). I used fish species to elaborate this method of grouping

sets of morphological characters with appropriate environmental variables. Subsequently, the validity of the environmental-morphological relationships were examined by applying the results of the analysis to a second group of fish species.

MATERIALS AND METHODS

Members of the Cyprinidae were used in this study because this speciose group exhibits a wide range of ecological preferences. Species of cyprinids were collected from the Red and Arkansas river drainages of the Mississippi river system. In a continuous drainage system, habitat preferences or requirements are important in determining species distributions. Individuals were collected with a seine (3.7 m long, 2 m deep, 3 mm mesh) from 124 locations in Oklahoma (Fig. 1) from 21 March through 21 June in 1978 and 1979. Environmental parameters were recorded for each sampled microhabitat at each location, then cyprinid individuals were collected and enumerated for each such microhabitat. A microhabitat was identified as an area homogeneous for water clarity, substrate type, presence of vegetation and cover, and water speed. I seined rather small areas to help ensure that different microhabitats were not sampled in the same seine haul.

Clarity was measured by Secchi disc depth in cm, and current as time in seconds for an object to float 5 m. Substrate type was scored from 0 to 5 (mud, sand, gravel, rubble, boulders, and bedrock, respectively). I assigned vegetation values from 0 to 5 (none, few filamentous algae, abundant filamentous algae, submerged macrophytes, floating macrophytes, emergent macrophytes). Cover (structure or vegetation in which fish may hide) was coded 1/0 for presence/absence, as was debris (presence or

absence of leaves or sticks on the bottom). Other environmental variables measured at each location included stream width and maximum stream depth (measured in meters), depth of the stream where fish were captured (in m), pH, and conductivity.

All individuals collected were preserved in 10% formalin and taken to the laboratory. Gut contents were divided into two categories (animal prey and detritus), and percentages of each category ascertained for all individuals measured. Detritus was principally composed of periphyton, although individuals of some species contained numerous substrate particles. Animal prey (usually invertebrates) was divided into three categories, scored 1 for terrestrial invertebrates (caught at the surface), 2 for open water prey (this included only zooplankton and fish) and 3 for benthos. Individuals with no prey items in their stomaches received no score, and were not included in further calculations involving this variable.

The first phase of this study (identification of morphological character sets and associated environmental variables) was pursued using 21 species of Notropis collected in Oklahoma (i.e., those marked with an asterisk in Table 1). The 29 measurements listed in Table 2 were taken from 5 to 40 individuals of each species. Body measurements and terms follow Lagler et al. (1977). Measurements of brain lobes follow Davis and Miller (1967). Center of gravity was determined by marking the spot on the side of the fish where, when pierced by a horizontally held needle probe, head and tail remained in the horizontal plane. Fin distances from the center of gravity were measured from this point to the anterior insertions to the body. Lagler et al. (1977) identified the scale row along which the scales are counted for assessment of the meristic

character called "scales above the lateral line." Scale length was the anterior-posterior length of the third scale from the dorsal end of this row. Length of the lateral stripe was expressed as the percentage of standard length included by the stripe. Peritoneal pigmentation was coded as percentage of inner body wall covered by melanophores. Brain lobe measurements, air bladder length, scale length and gill-raker number and length were assessed with a semi-automatic craniometer (Anderson 1968). Other measures were taken with a metric caliper. Length-related variables were converted to ratios with standard length. Brain measures were transformed as follows: For each lobe, length was multiplied by width to approximate lobe area. An index of brain area was established by multiplying twice the optic lobe width (brain width) by brain length. Lobe areas were then standardized by dividing each by brain area, i.e., expressing the lobe area as a fraction of the area of the brain. The square root of this fraction was used in further analyses, because brain-lobe ratios were two-dimensional, whereas all other ratios were of one-dimensional measures.

The SAS package of computer programs (Statistical Analysis System, Barr et al. 1976) was used for the statistical analyses described below. For each of the 21 Notropis species, means for ratios were calculated over all individuals. The means were then transformed to their natural logarithms. Mossiman and James (1979) discussed the use of logarithms in morphological studies involving allometric growth.

Environmental values for all locations where a given species was obtained were averaged across all individuals of that species. This procedure weighted the environmental values of those locations where the

species was most abundant. On the assumption that a species is most abundant in locations where environmental conditions best meet its requirements, I have considered that the weighted means for these parameters represent the species' "preferences." In further discussion, this estimate of a species' preference for an environmental parameter state will be termed its "field-observed preference." For data coded 1/0 (presence/absence) the result of this weighting gives the percentage of individuals of the species that occurred where that variable was coded "1". Because pH is a power function (negative logarithm of hydrogen ion concentration) geometric means of pH values were used (Sokal and Rohlf 1969). The resulting raw data matrix included 21 species and 37 variables (i.e., 24 morphological measures and 13 field-observed preferences).

A correlation matrix among variables was generated from this basic data matrix and subjected to principal components analysis. The principal component model is one of several factor analytic models, and may be the most appropriate when sample sizes are small (as was the case here). The principal component model involves a smaller number of latent variables, and hence the number of assumptions required by the model is smaller than for the common factor model (Mulaik 1972). Principal component analysis expresses the correlation among variables in terms of underlying "components"--uncorrelated, artificial variables that are linear compounds of the observed variables. The observed variables are variously correlated to the components. These correlations are referred to as "loadings." The matrix of component loadings was rotated by the Varimax method, giving a more easily interpretable "simple structure."

Principal components solutions are often left unrotated. The first component in an unrotated solution represents an axis that explains the maximum amount of variance among all observations. Each successive component is orthogonal to the preceding components and explains the maximum amount of the variance left unexplained by preceding components.

The maximum variance solution may not necessarily allow easy interpretation of the relationships among variables. Psychologists, who pioneered the use of factor analytic models, developed a set of criteria for rotation to simple structure, resulting in a representation of the components where only a few, interrelated variables are highly loaded on each component (Mulaik 1972). In this study, loadings of the observed variables on rotated components were interpreted under the following guidelines: A variable that correlated to a component at an absolute value of 0.70 or greater was judged to be highly related to that component; a variable that correlated at less than 0.40 was considered not to be associated to that component. Only those components with high loadings of more than two variables were interpreted. Given the assumptions of principal components analysis, a component may be interpreted in reference to those variables that correlated most highly with it. Variables that load heavily on a component share an attribute among themselves that is not shared with variables not correlated with that component. Therefore, components to which morphological and environmental variables correlated highly were interpreted as reflecting the functional associations of morphological and environmental variables.

The second phase of the analysis consisted of testing the predictability of environmental-morphological associations elucidated in

phase 1. For a component with high loadings for both environmental and morphological variables, the most heavily loaded environmental variable was regressed against the three morphological variables that loaded most heavily on the component. The resulting regression equations were used to predict the values of environmental variables for a new set of cyprinid species. This set, referred to as the cross-validation set, included those Notropis species that were only collected from 20 locations in Mississippi, and all non-Notropis cyprinids collected in Oklahoma and Mississippi. Field methods and laboratory procedures were the same for the test species (those species not marked by an asterisk in Table 1) as for the original set of Notropis species. However, only those morphological characters necessary for the regression equations were measured from the test species. Predicted environmental preferences were calculated for each test species by inserting the morphological means into the regression equations. Finally, predicted values were correlated to actual field-observed preferences (Pearson product-moment correlation and Kendall rank correlation).

RESULTS

Table 1 gives the means of environmental variables for all species used in this analysis. The results of the principal components analysis are shown in Table 3; only those variables with loadings of 0.40 or greater are shown. Components I, II, V, and VIII had substantial loadings for morphological characters and environmental parameters, indicating possibly interpretable relationships between the two sets of variables. Equations were then constructed that predicted values of the environmental variable most highly related to the component, using the

three morphological variables that loaded most highly. In one case, only two morphological variables loaded on a component at values greater than 0.40 (Table 3). Only these two variables were used in that regression equation. Calculated regressions derived from components I, II and VIII were significant, while the regression derived from component V was not. Pearson product-moment correlation coefficients associated with the three regressions (hereafter referred to as correlations) and Kendall rank correlations (hereafter referred to as rank correlations) were significant for the original 21 species of Notropis. Significant correlations for this set of species would be expected, as the regression predicting environmental preferences were generated from that set of data.

Component I identified an association between lateral stripe length, relative optic lobe area, vegetation, cover and debris. Other variables were only weakly correlated with this component. Equation 1 below was calculated by the least squares method, relating vegetation type to lateral stripe length and relative optic lobe area.

(1) Vegetation = 13.694 + 1.0207xBAND + 15.3544xLOPTIC

This relationship associates preference for more vegetation with a longer lateral stripe and relatively larger optic lobes. Table 4 shows the rankings of the test species according to the predicted value of vegetation, and gives the actual values of vegetation preference for these species. Neither of the correlations (given in Table 4) were significant for the test species when the equation was cross-validated.

Component II identified an association between prey location, relative body depth, relative scale length, relative lengths of the pelvic and dorsal fins, relative intestine length, and relative distance

from the center of gravity to the dorsal origin. This component was taken to represent a preference for an open-water versus a benthic feeding habit. Thus, all test species that were detritivores were given a value of 3.0 for this variable, assuming detritus was always foraged from the bottom. Equation 2 expresses this relationship.

(2) Prey = 0.2361 + 0.4533xLPELV - 0.2550xLDORS - 0.9168xLDRCN

Component II related a benthic habit to relatively longer pelvic fins, a longer dorsal fin, a longer intestine, large scales, and to a relatively small distance from the center of gravity to the dorsal origin. Table 6 gives the ranks of test-species according to predicted values of prey (benthic vs. open-water habit), and gives the mean values of prey location. The correlation between actual and predicted values of prey location was 0.52 ($P < .01$); the rank correlation was 0.42 ($P < .01$).

Component III associated water clarity, current speed, stream width and stream depth. This component differentiated species preferring large streams (with low clarity and current, and large depth and width) from those preferring small, clear streams with fast current. Component IV had substantial loadings for only two variables and was not interpreted.

Component V identified relative width, eye size, caudal peduncle depth, and vagal and facial lobe size, as relating to substrate preference. Regression equation 3 was derived from this association.

(3) Substrate type = -4.2571 + 1.3101xLEYE - 3.3359xLVAGAL
- 1.5819xFACIAL

This regression was not significant for the original Notropis species, and was therefore not cross-validated with the second set of cyprinid

species. This component associated occurrence over finer substrates with a relatively wide body, smaller eye, deeper caudal peduncle and larger vagal and facial lobes. Since the regression was not significant, no ranking of test species was done.

Component VI had large loadings for only two variables. Component VII had substantial loadings for morphological characters only.

Component VIII associated peritoneum pigmentation, relative intestine length and relative cerebellum area to percentage of detritus in the gut. The following equation expresses this relationship.

(4) Percent detritus = 7.5603 - 37.0343xLCEREB + 31.99xLINT + 2.3531xPRTNM

In this case, high values for peritoneum pigmentation and relative intestine length and small values for relative cerebellum area predict high values for percent detritus in the gut. Table 8 gives the rank of test species according to predicted values of detritus, and includes predicted and actual values. The correlation between actual and predicted values of detritus was 0.91 ($P < .01$), and rank correlation was 0.71 ($P < .01$). Predicted and actual values for vegetation preference, prey location and percent detritus for the original set of Notropis species are given in Felley (1980, Appendix A).

For a final analysis of the demonstrated relationships between the environmental and morphological character sets, I pooled the data for all cyprinid species. This resulted in a data matrix containing 26 characters (13 morphological characters measured from all cyprinid species, and the 13 environmental variables) for each of 43 cyprinid species. A matrix of correlations among characters was calculated from this data matrix.

Felley (1980) presented the matrix of intercorrelations between environmental and morphological variables. One test of the relationship between the morphological and environmental variables is a test that all canonical correlations between these two sets of variables are simultaneously zero. This test (Wilks-Lambda test, Morrison 1967) is also a test of the null hypothesis that the matrix of intercorrelations between sets is a matrix of zeros. The canonical correlations between the morphological and environmental variable sets were quite high (the first three were 0.97, 0.93 and 0.82, respectively), but were not significantly different from zero. This is due to the small number of observations (species) from which the correlation matrix was calculated. Despite the size of the canonical correlations, the test did not have the power to detect a relationship between the sets of morphological and environmental variables.

DISCUSSION

The principal components analysis was successful in identifying covarying sets of environmental and morphological variables. The analysis is of morphological character states related to environmental preferences. I defined a field-observed preference, but preferences established in laboratory experiments (e.g., Matthews and Hill 1979) would be equally valid in such a study. A number of studies (Sokal and Daly 1961, Sokal et al. 1961, Atchley 1971, Stevenson et al. 1974, Sokal et al. 1980) have used factor analysis procedures to aid in the identification of independent variables and their concomitant dependent variables. Environmental preferences are dependent assuming that morphological adaptations are determiners of a species' choice of habitat. The following

is a discussion of the environmental (dependent) variables and their relationships to each associated set of morphological (independent) variables. Several authors (Miller and Robison 1975, Pflieger 1975, Douglas 1974) present information on the species used in this study. I have used their observations in forming my interpretations and conclusions.

Component I identified a relationship between preference for vegetation, cover and debris, and extent of the lateral stripe and relative optic lobe area. Nikolskii (1963) considered species with lateral stripes to be schooling forms, the stripe aiding in orientation of individuals and confusion of predators. However, all of the Notropis species analyzed in the first part of this study may school, yet the species have stripes of variable lengths. In the cyprinid species studied here, the stripe may serve as disruptive camouflage coloration (Cott 1940). In a visually complex environment (with large amounts of vegetation, cover and debris) an extensive lateral stripe may serve to confuse predators, as Nikolskii (1963) hypothesized for schooling prey species. Species living in vegetation might derive more protection from disruptive coloration than species living in open water.

Optic lobe size reflects the importance of vision to the fish (Evans and Miller 1965). Species living in structurally complex environments (as in vegetation) might be better served by larger optic lobes. Large optic lobes may also reflect a preference for high water clarity; species living in turbid water may not require good vision, and algae and submerged macrophytes do not grow in turbid water. Water clarity did not load on this component, however. The Pearson correlation was not significant for predicted and actual values of vegetation

preference, while the rank correlation was significant only at the 0.09 level. However, the rankings given in Table 4 seem to conform to the known biology of the test species. The three lowest ranked forms are highly specialized benthic feeders. Of the four lowest ranked species, Hybopsis aestivalis, Hybognathus placitus and Pimephales vigilax are benthic feeders common in extremely turbid waters. In contrast, such species as Notemigonus crysoleucas, Notropis texanus, Phoxinus erythrogaster and Hybognathus hayi (often found in vegetation) received high ranks. Most individuals of Nocomis asper that I collected were young-of-the-year, or two years old. Pflieger (1975) stated that young Nocomis prefer vegetation and cover. Their morphology agrees with this, as they have relatively larger eyes than adults and have a complete lateral stripe, which is lost in adults.

Component II identified an association of relative size of scales and fins, and dorsal fin position, with prey location. It became apparent from these results that the variable "prey location" was actually measuring an aspect of a species' preferred depth in the water column, rather than actual prey choice. Aleev (1969) noted that the farther caudad from the center of gravity the dorsal fin is placed, the more effective it is as a stabilizer and the less it acts as a rudder. Fish species having morphologies that allow high maneuverability are characterized by larger fins and a dorsal fin acting as a rudder. Active-swimming species tend to be more stream-lined, having smaller fins. In these more active swimmers, the dorsal fin is placed behind the center of gravity and acts as a stabilizer. Among the cyprinids used in this study, the active swimmers tended to be less deep-bodied than the

maneuverable species, adding to the body stream-lining of the active swimmers. These results suggest that cyprinids with a preference for proximity to the substrate have morphologies allowing high maneuverability. Intestine length may load heavily on this component because species with benthic habits include those that feed primarily on detritus; these forms are characterized by long intestines. Open-water feeders fed more on terrestrial insects, and consequently had low values for prey location. Species preferring proximity to the substrate had high values for prey location, as they mostly ate benthic invertebrates (Table 6). The derived nature of this variable may cause some of the ambiguity reflected in the low (though significant) correlations. Rather than assessment of stomach contents, direct observation of species should give a better estimate of a species' preferred depth in the water column. The rankings of test species (Table 6) suggest that while not ideal, the derived "prey location" variable gives good representation of water depth preferences of these species. Semotilus atromaculatus, Notemigonus crysoleucas, Notropis roseipinnis, and Pimephales promelas are open-water forms. By contrast, all the species of Hybognathus, Notropis longirostris, Hybopsis x-punctata and Phenacobius mirabilis are strictly benthic forms. Inspection of mouthparts might have allowed these interpretations (Keast and Webb 1966); fin placement and relative fin size give similar information about the habits of these species. Scale size may relate to a benthic versus an open-water habit; species frequently contacting the substrate may have larger, more robust scales that minimize scale loss.

Component III indicates the interrelationships of field-observed preferences among the species; it separates species characteristic of

headwaters from species found primarily in large rivers. Species tolerating turbidity and not preferring current were found in larger rivers, while fast water forms known to prefer clear water were found in smaller, upstream creeks and streams. However, the analysis found no morphological characters associated with this set of field-observed preferences.

Component VIII related peritoneum pigmentation, relative intestine length and cerebellum area to amount of detritus present in the gut. A black peritoneum and a long intestine are usually found in herbivorous forms, and have been presumed to be adaptations for herbivory (Snelson 1971). The results presented here support this conclusion. A relatively large cerebellum is characteristic of active forms (Evans and Miller 1967). It may be that herbivorous cyprinids are more sedentary than those that must actively chase their prey, and their relatively smaller cerebella reflect a less active life-style. For the species used in cross-validation of the regression equation, rank and product-moment correlations were very high. The test species rankings (Table 6) conform to our knowledge of these species' natural histories.

Component V associated substrate preference with relative body width, eye size, caudal peduncle depth, and vagal and facial lobe area. Species found over fine substrates had relatively wider bodies, smaller eyes, deeper caudal peduncles, and larger vagal and facial lobes than forms found over rock substrates. Davis and Miller (1965) characterized species with enlarged vagal and facial lobes as being taste feeders, as opposed to sight feeders which had enlarged optic lobes. Optic lobe area did not load on this component, but eye size did; those forms having

enlarged facial and vagal lobes generally had relatively smaller eyes. Caudal peduncle depth is decreased in actively swimming forms, as well as in forms living in fast water (Gatz 1979b). Body width in cyprinids may be associated with water speed as well. This component separates species found in slow-moving, turbid waters from those preferring swifter water. Species in slow water are found more often over fine substrates, since these substrates do not occur in swift flowing waters. The morphological trends suggested by component V differentiate taste-feeders found in slow water from sight feeders found in clearer, swifter water. The environmental-morphological relationships demonstrated by this component, though interpretable, were not strong enough to allow prediction for the test species.

Three criteria for validating aspects of this method have been presented in my study. First, if given morphological characters are in fact adaptations to different environmental parameters (in a group of species), then morphological and environmental variables should appear together when data from this group are subjected to a procedure grouping related variables. In different situations, exploratory statistical methods other than principal components analysis might be more appropriate. Second, the adaptations identified by the factor analytic procedure should conform to what is known of functional fish morphology. The extensive knowledge of fish functional anatomy was one of the bases of this study. Finally, can the results of such an analysis be used to predict environmental preferences for a different group of species?

The method satisfied these three criteria. First, several components demonstrated associations between environmental and morphological

characters. Second, in most cases the method identified known adaptations to environmental parameter states. Some speculation was necessary to explain the association of lateral stripe length and optic lobe area with vegetation, as well as the relationship of scale size to a benthic versus an open-water habit. In the case of component V, my explanation was in terms of adaptations to levels of water clarity and current speed. However, among the environmental variables, only substrate type loaded highly on this component. Substrate type is an indicator of water current history in an area, and is related to water clarity (Hynes 1970). The other relationships found in this analysis are well substantiated by the large body of literature on fish functional anatomy. Satisfying the final criterion for success was made more difficult because this analysis identified morphological adaptations to environment in species of one genus, then extrapolated the results to other genera of an ecologically very diverse family. In two of the three cases, predicted environmental values were significantly correlated to field-observed preferences, and in two out of three cases, the rank correlations were significant. One rank correlation (that of predicted with actual vegetation preference) was near significance ($P < 0.09$). Though not significant, the rankings of test-species for this environmental preference still reflected these species' biology. Only one prediction equation failed outright, that relating substrate type to relative body width, eye length, caudal peduncle and vagal lobe area. However, this relationship was still interpretable, though no predictions were possible for the test-species.

On the basis of the three criteria outlined above, the method presented here successfully identified morphological adaptations to

environmental parameter states for a group of species. If another set of species were to be investigated, it would be wise to validate the demonstrated associations as was done here. The substrate type-morphology association, though interpretable and possibly reflective of some morphological relationships with substrate type in the genus Notropis, was not strong enough to give useful information about the rest of the Cyprinidae. Additional notes on this method follow. (1) The principal components analysis used to identify relationships assumed uncorrelated, orthogonal components. Sokal et al. (1980) found that different factors that demonstrated environmental-physiological relationships were orthogonal. In many cases, this assumption may not be biologically meaningful. An oblique rotation of the component loading matrix gave similar results to the orthogonal Varimax rotation in my study, but some differences were apparent. Most of the variables (both morphological and environmental) loaded heavily on the first component in the obliquely rotated solution. Also, no component appeared relating percent of detritus in the gut with morphology, as was seen in the orthogonal rotation. (2) This procedure started with a matrix of correlations among variables which summarized linear pairwise relationships among variables. Again, an assumption of strictly linear relationships may not be appropriate. (3) Factor analysis procedures require large sample sizes to obtain accurate representations of the factors. In an analysis such as mine, "sample size" is the number of species being investigated. Artifacts due to small sample size are another reason to test the results of factor analysis with multiple regression. Multiple regression gives a statistical substantion of the association of variables demonstrated

in a given factor.

The procedure outlined here may be useful in identifying morphological-environmental relationships in a number of different situations. This method may also aid in understanding the nature of adaptations in poorly known groups. Conversely, it can be used to test our understanding of adaptations in groups that we feel we know well, allowing an independent assessment of morphological-environmental associations. Studies such as this may serve a similar function for species that for some reason may not be characterizable ecologically. Finally, such studies may provide a framework for testing the assumption of studies of niche metrics based on species morphology.

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Figure 1. Collection locations in Oklahoma. Squares represent localities where species of Notropis only were collected. Circles represent localities where both Notropis and non-Notropis cyprinids were collected.

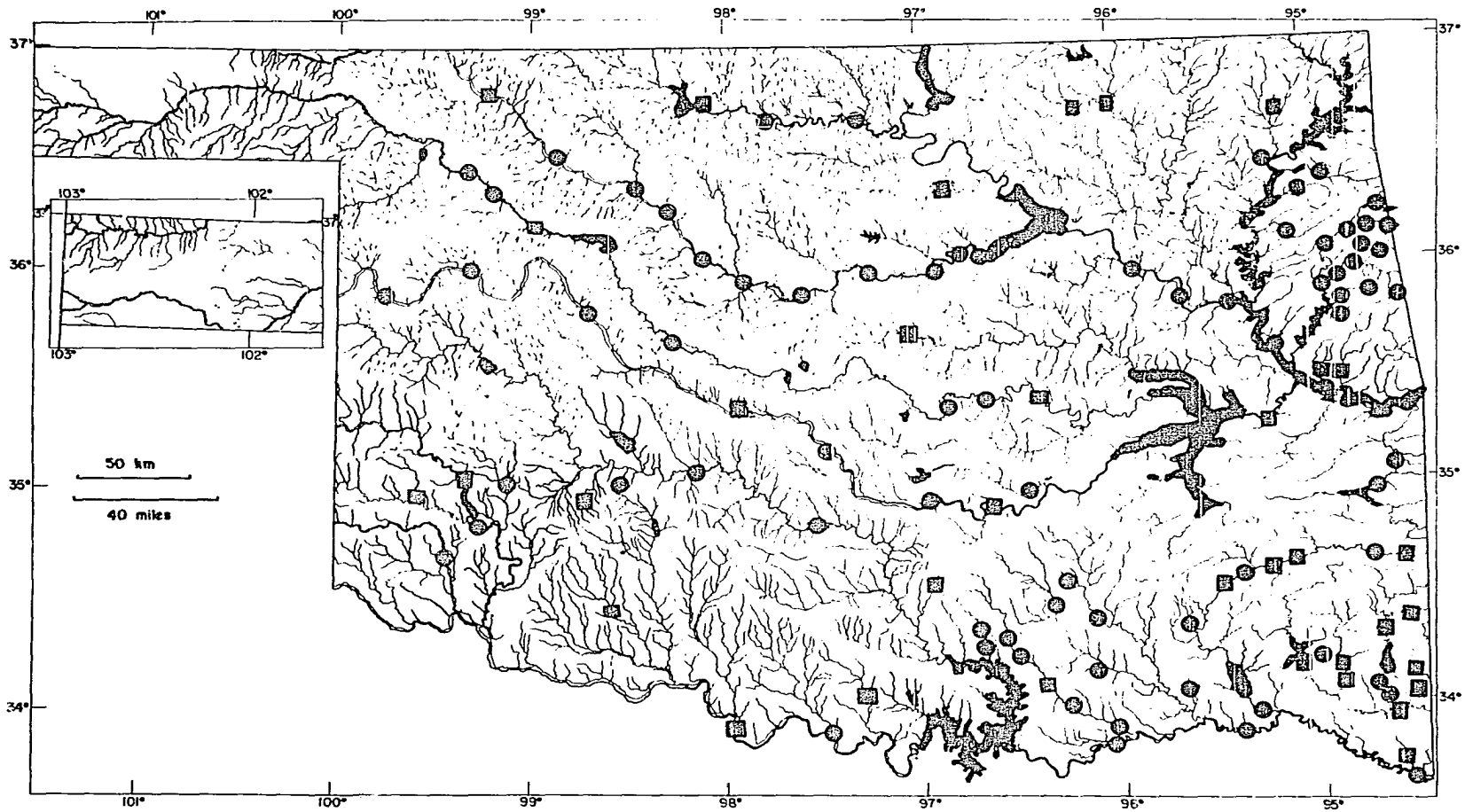
101°
100°
99°
98°
97°
96°
95°
37°
36°
35°
34°
103°
102°
50 km
40 miles

Table 1. Means for environmental variables over all individuals collected of each species. Measurements and coded variables are described in the text.

Species	N	Clarity	Vegetation type	Substrate type	Cover	Debris	Current speed	Stream depth	Stream width	Capture depth	pH	Conductivity
Campostoma anomalum	73	180.4	0.01	1.81	0.41	0.07	39.0	1.21	19.0	0.42	7.4	145.9
Dionda nubila	85	190.3	0.00	2.51	0.47	0.38	42.2	1.35	19.9	0.47	7.3	143.6
Hybognathus hayi	2	50.0	0.00	1.00	1.00	1.00	90.0	1.64	9.8	0.66	7.7	80.0
H. nuchalis	4	112.5	0.00	1.00	0.00	1.00	90.0	1.64	16.4	0.98	7.3	35.0
H. placitus	64	23.7	0.00	0.84	0.11	0.00	50.1	1.31	41.7	0.75	7.5	11,538.1
Hybopsis aestivalis	1	3.0	0.00	1.00	0.00	0.00	7.5	0.98	13.1	0.33	8.0	800.0
H. amblops	3	150.0	0.00	1.50	0.33	0.00	40.0	1.21	19.4	0.85	7.4	80.0
H. x-punctata	2	200.0	0.00	2.00	0.00	0.00	12.0	1.31	13.0	0.33	8.0	100.0
Nocomis asper	17	89.5	0.59	1.88	0.29	0.35	75.3	1.11	20.0	0.40	7.8	187.1
N. leptocephalus	3	200.0	3.00	1.00	1.00	1.00	90.0	0.98	6.5	0.98	5.5	30.0
Notemigonus crysoleucas	13	57.5	0.77	1.19	0.38	0.15	75.0	1.15	31.4	0.83	7.6	369.2
Notropis atherinoides*	226	20.5	0.00	0.80	0.19	0.03	67.8	1.53	78.9	0.71	7.6	2,551.6
N. bairdi*	96	17.0	0.00	0.70	0.00	0.00	34.5	1.25	32.4	0.78	8.6	12,218.2
N. boops*	676	154.0	1.44	2.34	0.75	0.37	66.1	1.14	19.9	0.71	6.0	80.3
N. buchanani*	13	12.5	0.00	0.42	0.00	0.00	90.0	3.18	320.8	1.03	7.5	858.5
N. camurus	20	200.0	0.00	2.00	0.00	0.00	30.0	0.98	13.1	0.66	7.8	40.0
N. chrysocephalus*	49	146.7	0.80	2.29	0.57	0.34	66.4	1.35	8.3	0.60	6.0	120.1
N. emiliae*	5	151.8	1.80	1.50	0.80	0.80	78.0	1.38	15.1	0.98	5.7	34.0
N. fumeus*	84	156.4	1.76	4.00	0.56	0.00	90.0	1.60	43.6	0.71	7.7	30.3
N. girardi*	46	129.7	0.00	2.00	0.33	0.00	12.7	1.41	24.0	1.04	6.8	150.0
N. greenei*	12	126.7	0.00	2.00	0.33	0.00	12.5	1.41	24.0	1.09	6.8	150.0
N. longirostris	28	162.5	0.00	1.23	0.29	0.10	66.9	0.95	15.9	0.66	7.2	36.4
N. lutrensis*	984	42.4	0.19	0.99	0.15	0.06	69.0	1.12	54.1	0.55	7.7	2,044.3
N. ortenburgeri*	5	160.0	4.00	1.00	1.00	0.80	90.0	1.18	6.0	0.85	5.1	38.0

Table 1. (cont.).

Species	N	Clarity	Vegetation type	Substrate type	Cover	Debris	Current speed	Stream depth	Stream width	Capture depth	pH	Conductivity
N. perpallidus*	23	133.8	0.00	3.91	0.00	0.00	32.5	1.92	22.3	0.96	6.8	30.1
N. pilsbryi*	276	186.2	0.02	1.93	0.31	0.25	46.3	0.94	15.7	0.59	7.2	124.6
N. potteri*	110	6.1	0.00	0.91	0.93	0.01	90.0	1.91	189.3	0.67	7.1	241.5
N. roseipinnis	222	193.2	1.19	0.96	0.48	0.92	62.9	1.09	4.8	0.82	6.1	45.0
N. rubellus*	75	96.9	0.00	2.21	0.15	0.11	58.5	1.36	19.8	0.60	7.2	191.7
N. shumardi*	13	19.8	0.00	0.46	0.00	0.23	90.0	1.77	209.0	0.78	7.5	229.2
N. stramineus*	61	174.2	0.00	0.57	0.87	0.02	87.1	0.30	6.4	0.23	7.3	435.9
N. texanus	6	145.0	0.00	0.75	0.00	1.00	90.0	1.80	19.6	1.14	8.3	60.0
N. umbratilis*	247	142.1	1.89	2.43	0.61	0.40	68.9	1.25	18.4	0.77	5.7	70.0
N. venustus*	31	92.2	0.00	1.74	0.35	0.23	58.5	1.13	19.1	0.58	7.0	293.7
N. volucellus*	464	127.4	0.01	3.86	0.01	0.03	32.0	1.93	23.0	0.99	6.8	37.5
N. whipplei*	132	155.7	1.55	2.22	0.71	0.16	61.6	1.08	20.5	0.69	7.0	86.3
Phenacobius mirabilis	13	8.0	0.00	4.00	0.00	0.00	10.0	0.16	19.7	0.16	8.6	1,100.0
Phoxinus erythrogaster	50	200.0	0.10	1.93	0.14	0.26	25.1	0.76	4.1	0.71	7.1	122.5
Pimephales notatus	30	38.8	0.40	1.73	0.13	0.10	80.5	0.97	13.3	0.38	6.4	252.5
P. promelas	9	200.0	0.00	0.50	1.00	0.00	90.0	0.16	2.6	0.16	7.3	340.0
P. tenellus	6	50.0	0.00	0.50	0.00	0.00	20.0	1.31	32.8	0.33	6.5	175.0
P. vigilax	33	21.8	0.00	0.66	0.21	0.48	70.8	1.66	60.6	0.65	7.4	612.7
Semotilus atromaculatus	4	200.0	0.00	2.00	0.50	0.00	90.0	0.66	2.0	0.33	7.6	140.0

*Species used in first phase of analysis.

Table 2. Morphological measurements and abbreviations used in the text. Terms Lagler et al. (1977). Abbreviations beginning with an "L" refer to the natural logarithm of ratios (character length/ standard length or lobe area/brain area). See text for further explanation.

Abbreviation	Measurement
LDEPTH	Body depth
LWIDTH	Body width
LEYE	Eye length
LCAUD	Least depth of the caudal peduncle
LPECT	Pectoral fin length
LPCTCN	Distance of the pectoral fin base from the center of gravity
LPELV	Pelvic fin height
LPLCN	Distance of the pelvic fin base from the center of gravity
LDORS	Dorsal fin height
LDRCN	Distance of the dorsal fin base from the center of gravity
LCDWTH	Distance from the caudal fin base to the fork of the caudal fin
LSCALE	Scale length (see text for identification of the scale)
LMOUTH	Mouth height
RAKER	Gill raker number on the outermost gill arch
LRKRL	Length of the longest gill raker
BAND	Lateral stripe length
PRTNM	Peritoneum pigmentation
LINT	Intestine length
LAIR	Airbladder length
LCEREB	Cerebellum length and width
LOPTIC	Optic lobe length and width
LVAGAL	Vagal lobe length and width
LFACIAL	Facial lobe length and width
	Standard length
	Brain length (from the anterior end of the olfactory lobes to the posterior end of the vagal lobes)

Table 3. Results of principal components analysis on all morphological and environmental variables, except LSPAN. Only characters with high loadings are shown. Abbreviations follow Table 1.

Variable	Factor							
	I	II	III	IV	V	VI	VII	VIII
BAND	.48							
LOPTIC	.54							
LDEPTH		.57						
LPELV		.90						
LDORS		.80						
LDRCN		-.86						
LSCALE		.69						
LMOUTH				.56				
LWIDTH					.44			
LEYE					-.86			
LCAUD					.46			
LVAGAL					.61			
LFACIAL					.68			
LCDWTH						.59		
LRKRL						.88		
LPECT							.52	
LPCTCN							-.88	
LPLCN							.61	
LAIR							-.61	
PRTNM								.79
LINT		.59						.55
LCEREB								-.54
Vegetation	.93							
Cover	.72							
Debris	.87							
Prey		.82						
Clarity			-.71					
Current			.57					
Stream width			.93					
Stream depth			.69					
Capture depth				.90				
Substrate type					.50			
% Detritus								.74

Table 4. Test-species ranked by predicted values of vegetation, with actual values given. Pearson product-moment correlation coefficient is 0.16 ($P < .47$), Kendall rank correlation coefficient is 0.29 ($P < .09$).

Species	Vegetation	
	Observed	Predicted
Hybopsis aestivalis	0.00	-3.63
Hybognathus placitus	0.00	-0.62
Notropis longirostris	0.00	-0.24
Pimephales vigilax	0.00	-0.12
Hybognathus nuchalis	0.00	0.37
Notropis camurus	0.00	0.38
Campostoma anomalum	0.01	0.40
Semotilus atromaculatus	0.00	0.41
Hybopsis x-punctata	0.00	0.42
Phenacobius mirabilis	0.00	0.48
Pimephales notatus	0.40	0.53
P. tenellus	0.00	0.66
Nocomis leptocephala	3.00	0.66
Hybopsis amblops	0.00	0.67
Notropis roseipinnis	1.19	0.67
Notemigonus crysoleucas	0.77	0.70
Nocomis asper	0.59	0.71
Pimephales promelas	1.00	0.83
Hybognathus hayi	0.00	1.02
Notropis texanus	0.00	1.11
Phoxinus erythrogaster	0.10	1.25
Dionda nubila	0.00	1.28

Table 5. Test-species ranked by predicted values of prey location, with actual values given. Pearson product-moment correlation coefficient is .48 ($P < .03$), Kendall rank correlation coefficient is .49 ($P < .001$).

Species	Prey location	
	Observed	Predicted
Semotilus atromaculatus	1.00	1.80
Notropis roseipinnis	1.45	1.98
Notemigonus crysoleucas	2.29	2.08
Phoxinus erythrogaster	3.00	2.08
Nocomis asper	3.00	2.10
Pimephales promelas	2.33	2.39
P. tenellus	2.67	2.40
P. notatus	3.00	2.51
Dionda nubila	3.00	2.52
Notropis camurus	1.80	2.57
Campostoma anomalum	3.00	2.59
Nocomis leptocephala	3.00	2.74
Notropis texanus	2.83	2.74
Pimephales vigilax	3.00	2.88
Hybognathus placitus	3.00	2.91
Hybopsis aestivalis	3.00	2.95
Notropis longirostris	2.91	3.00
Hybognathus nuchalis	3.00	3.42
H. hayi	3.00	4.29
Hybopsis x-punctata	3.00	4.62
H. amblops	3.00	4.75
Phenacobius mirabilis	3.00	4.80

Table 6. Test-species ranked by predicted percentage of detritus in the gut, with actual values given. Pearson product-moment correlation coefficient is 0.91 ($P < .001$) and Kendall rank correlation coefficient is 0.71 ($P < .001$).

Species	Percent Detritus	
	Observed	Predicted
Notropis roseipinnis	0.00	7.33
Hybopsis aestivalis	0.00	8.71
Notropis longirostris	17.11	9.31
N. texanus	11.67	9.71
Phenacobius mirabilis	16.67	13.18
Hybopsis amblops	33.33	16.28
Notropis camurus	26.67	18.39
Notemigonus crysoleucas	40.00	21.18
Semotilus atromaculatus	0.00	22.45
Pimephales vigilax	48.33	24.37
P. tenellus	0.00	25.58
Nocomis asper	8.57	28.42
Pimephales notatus	55.25	37.05
Nocomis leptocephala	80.00	49.48
Hybopsis x-punctata	65.00	53.88
Phoxinus erythrogaster	46.66	55.67
Pimephales promelas	70.00	60.29
Dionda nubila	94.05	71.19
Hybognathus nuchalis	75.00	75.62
H. hayi	96.67	78.52
H. placitus	100.00	83.64
Campostoma anomalum	100.00	90.10

Appendix A: Predicted and actual values of vegetation type, prey location, and percent detritus in the gut, for the set of 21 Notropis species collected from Oklahoma, on whom the principal components analysis was run.

A (I). *Notropis* species used in the principal components analysis, ranked by predicted values for vegetation preference.

Species	Vegetation	
	Observed	Predicted
Notropis girardi	0.00	-0.45
N. bairdi	0.00	-0.36
N. buchanani	0.00	0.25
N. atherinoides	0.00	0.01
N. stramineus	0.00	0.24
N. shumardi	0.00	0.27
N. lutrensis	0.20	0.29
N. perpallidus	0.00	0.48
N. potteri	0.02	0.48
N. rubellus	0.00	0.61
N. boops	1.40	0.68
N. venustus	0.00	0.71
N. umbratilis	1.89	0.71
N. volucellus	0.01	0.73
N. whipplei	1.55	0.87
N. chrysocephalus	0.80	0.92
N. greenei	0.00	1.08
N. fumeus	1.76	1.09
N. pilsbryi	0.02	1.74
N. emiliae	1.80	1.77
N. ortenburgeri	4.00	1.81

A (2). *Notropis* species used in the principal components analysis, ranked by predicted values for prey location. Actual values are given as well.

Species	Prey location	
	Observed	Predicted
Notropis fumeus	1.52	1.74
N. atherinoides	1.86	1.93
N. rubellus	1.75	1.94
N. umbratilis	1.72	1.96
N. lutrensis	2.37	2.19
N. venustus	2.33	2.28
N. volucellus	2.89	2.32
N. potteri	2.67	2.34
N. greenei	2.50	2.35
N. whipplei	2.52	2.39
N. boops	2.39	2.42
N. shumardi	1.75	2.44
N. perpallidus	2.44	2.46
N. bairdi	2.35	2.46
N. pilsbryi	2.92	2.48
N. girardi	2.89	2.49
N. ortenburgeri	2.20	2.53
N. stramineus	2.88	2.61
N. buchanani	2.46	2.83
N. emiliae	2.75	2.98
N. chrysocephalus	3.00	3.02

A (3). *Notropis* species used in the principal components analysis, ranked by predicted values for detritus in the gut. Actual values are given as well.

Species	Percent Detritus	
	Observed	Predicted
Notropis perpallidus	7.50	-3.35
N. fumeus	0.00	3.70
N. umbratilis	0.00	4.74
N. rubellus	1.75	5.42
N. atherinoides	6.03	7.25
N. emiliae	6.25	8.97
N. shumardi	11.00	9.80
N. buchanani	11.54	11.69
N. girardi	23.84	15.00
N. volucellus	28.05	15.07
N. potteri	8.28	15.21
N. ortenburgeri	11.67	15.79
N. venustus	2.63	16.14
N. lutrensis	21.16	17.31
N. bairdi	27.82	18.95
N. whipplei	23.92	20.85
N. greenei	24.83	20.92
N. stramineus	0.25	23.15
N. boops	31.47	29.41
N. chrysocephalus	30.62	32.12
N. pilsbryi	42.40	32.88

Appendix B. Correlations between the morphological and environmental characters measured for all 43 species used in this study.

Morphological characters	Environmental characters				
	Clarity	Vegetation	Substrate	Cover	Debris
BAND	.316	.372	.212	.302	.284
PRTNM	.441	.268	.048	.267	.232
LWIDTH	-.078	-.280	-.240	-.079	-.208
LEYE	.266	.245	.123	.134	.116
LCAUD	-.227	-.085	-.320	-.107	-.069
LPELV	-.159	-.047	-.194	.046	.135
LDORS	-.146	.086	-.252	.089	.173
LDRCN	.094	.176	-.017	.099	-.109
LSCALE	-.144	-.008	-.101	-.031	.106
LINT	.114	-.178	-.215	.129	.194
LCEREB	-.478	-.216	-.337	-.203	-.065
LOPTIC	.431	.246	.190	.328	.298
LVAGAL	-.149	-.107	-.433	.079	-.073

Appendix B, Continued.

Morphological characters	Environmental characters			
	Current	Stream depth	Stream width	Capture depth
BAND	.078	-.245	-.300	.066
PRTNM	.017	-.241	-.350	-.085
LWIDTH	-.124	-.348	.070	-.406
LEYE	.133	.275	.079	.430
LCAUD	.181	.028	.291	-.005
LPELV	.043	.120	.167	.090
LDORS	.090	.332	.313	.483
LDRCN	.250	.044	.068	.109
LSCALE	.026	.220	.127	.092
LINT	.023	-.127	-.166	-.217
LCEREB	.158	.229	.382	.201
LOPTIC	.320	.078	-.062	.184
LVAGAL	.060	-.067	-.056	-.027

Appendix B, Continued.

Morphological characters	Environmental characters			
	pH	Conductivity	Prey	Detritus
BAND	-.436	-.231	-.092	.001
PRTNM	-.275	-.051	.170	.651
LWIDTH	.292	.277	.355	.250
LEYE	-.356	-.365	-.233	-.384
LCAUD	.029	.248	.161	.038
LPELV	.055	-.069	.413	.153
LDORS	-.124	.078	.219	-.078
LDRCN	-.257	-.019	-.557	-.356
LSCALE	-.013	-.145	.381	.101
LINT	.117	.198	.461	.919
LCEREB	.290	.307	-.140	-.009
LOPTIC	-.245	-.302	-.074	.112
LVAGAL	.067	.368	.109	.252