17. The Importance of Phylogenetic Constraints in Comparisons of Morphological Structure Among Fish Assemblages

Richard E. Strauss

Abstract

Morphological approaches to the study of community relationships are based on the premise that morphological differences among organisms reflect in large part their ecological relationships and that morphological "space" can be mapped onto ecological "space." Although morphological characteristics have been used to account for aspects of foraging and habitat use, phylogenetic effects of form diversity on the repeatability of morphological patterns of variation among communities are unknown. The morphological structures of several North and South American freshwater fish assemblages were compared to assess the dependence of morphological congruence on taxonomic similarity. Correlations of morphological patterns are high (> 0.7) for geographically proximate assemblages, but for comparisons between North and South American assemblages the average correlation is 0.20. The density at which species are "packed" into morphospace, and thus the average similarity between species, is independent of the number of species present; within assemblages, therefore, total size-independent morphological variation is highly dependent on species diversity.

Hypotheses about patterns in natural communities, their structure and composition, are at the center of current ecological debate (Cody and Diamond, 1975; Wiens and Rotenberry, 1980a; Anderson et al., 1981; Strong, 1983; Salt, 1984; Strong et al., 1984). Important questions are the extent to which competitive interactions pattern the observed ecological and morphological relationships of species within communities, and to what degree the ecological functions (niches) of members can be predicted from their morphological characteristics. The assumption of strong correspondence between niche and morphology (that is, that morphological "space" maps directly onto ecological "space"; Hutchinson, 1968; Ricklefs and Travis, 1980) is critical to many community studies. For example, several researchers have compared patterns of morphological structure among communities (Ricklefs and O'Rourke, 1975; Findley, 1973, 1976; Gatz, 1979b; Ricklefs and Travis, 1980; Ricklefs et al., 1981) or expressed relative niche characteristics in terms of morphological differences among species (Hespenheide, 1973; Gatz, 1979a). Yet congruence between morphology and ecology is seldom tested directly (Felley, 1984; Miles and Ricklefs, 1984).

It is evident that morphological characteristics can be used to predict aspects of foraging behavior and habitat use (Flanagan, 1981; Gatz, 1979b, 1981; Findley and Black, 1983; Miles and Ricklefs, 1984). However, a considerable amount of residual morphological variation in many communities cannot be related directly to ecological variables (Weins and Rotenberry, 1980b; Felley, 1984), reducing the predictability of morphological relationships in one assemblage from those observed in another. An additional confounding factor is faunal composition: if the historical pool of taxonomic "morphotypes" has been very different for two assemblages—that is, if the communities being compared are comprised of species derived from sets of independent evolutionary lineages—then the resulting morphological patterns could differ profoundly. How might morphological structure be affected, for example, when characins are "substituted" (in a historical sense) for cyprinids? Two possibilities are (1) that ecological (e.g., hydrodynamic, foraging) factors are so important in sorting out sets of coexisting species that the major patterns of variation remain relatively stable among communities, irrespective of the actual species present, or (2) that differences in body form among major evolutionary lineages are large enough to override small-scale, localized ecological pressures, so that, for example, North American stream-fish communities might be structured very differently from corresponding South American communities. In the latter case some degree of correspondence in major patterns of morphological variation might be evident once phylogenetic constraints (taxonomic similarities) have been taken into account.
Table 17.1. Localities and Their Taxonomic Composition*

<table>
<thead>
<tr>
<th>Locality</th>
<th>Number of</th>
<th>Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Families</td>
<td>Genera</td>
</tr>
<tr>
<td>1. Little Fishing Creek, Pennsylvania</td>
<td>8</td>
<td>19</td>
</tr>
<tr>
<td>2. Yellow Breeches Creek, Pennsylvania</td>
<td>6</td>
<td>15</td>
</tr>
<tr>
<td>3. Lake Opinicon, Ontario</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>4. Big Sandy Creek, Texas</td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td>5. Martis Creek, California</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>6. Río Paraná, Paraguay</td>
<td>9</td>
<td>31</td>
</tr>
<tr>
<td>7. Río Aquidabán, Paraguay</td>
<td>5</td>
<td>21</td>
</tr>
<tr>
<td>8. Composite</td>
<td>22</td>
<td>22</td>
</tr>
</tbody>
</table>

*Taxa are given in the Appendix.

To explore such questions in detail, I initiated a study of morphological variation among freshwater fish assemblages collected from a variety of climatic regions and having varying degrees of taxonomic similarity to one another. Specifically, the study was designed to answer the following questions: (1) What are the major patterns of variation, independent of ontogenetic effects on body form, among fishes in stream assemblages? (2) Are patterns of variation consistent among assemblages from different habitats? (3) Is degree of concordance dependent on taxonomic composition? If so, at what taxonomic level? (4) Is the overall level of similarity, the degree to which species are “packed” into morphological space, dependent on the number or composition of species present? And does packing density differ for temperate versus subtropical habitats?

Materials and Methods

Localities and Taxonomic Composition

Localities were chosen to represent differing habitats and taxonomic assemblages (table 17.1). Assemblages were represented by series of fish collections taken within a limited region (less than 25 km linear extent) of the watershed. Localities and associated collections were selected from three different sources: personal records, selected literature records, and museum expedition records.

The two Pennsylvania localities (PA) were extensively sampled in 1978–79; all specimens were deposited in the Pennsylvania State University research collections. Lake Opinicon, Ontario (ON; Keast and Webb, 1966; Keast, 1978b), Big Sandy Creek, Texas (TX; Evans and Noble, 1979, stations 3–5), and Martis Creek, California (CA; Moyle and Vondracek, 1985) had been surveyed by the authors cited. On the basis of their species lists and descriptions, I located collections in the University of Michigan Museum of Zoology (UMMZ) that corresponded as nearly as possible to the cited geographical locations and that had been collected in similar habitat, especially lake versus stream (similar studies that lacked corresponding UMMZ collections were disregarded). These collections were considered to be representative of the described assemblages, under the reasonable assumption that intraspecific geographic variation is negligible in relation to ontogenetic and interspecific variation. The two Paraguayan (PY) localities were selected from a large survey conducted by the UMMZ Paraguayan Expedition of 1979. All specimens examined were taken directly from those collections.

Because the North American and the Paraguayan assemblages had virtually no faunal overlap, a composite sample was assembled by pooling data on one species from each of 22 families represented in the study (see Appendix). Species were chosen to maximize taxonomic overlap among localities. In several analyses of morphological structure this composite was treated as an independent assemblage, though the data comprising it were replicated from the other samples.

Measures of taxonomic similarity ($S$) among assemblages were based on Dice’s ($=$ Sorensen’s) index, $S = 2N_1/(N_1 + N_2)$, where $N_1$ and $N_2$ are the numbers of taxa in two assemblages and $N$ is the number held in common. The index ranges from 0 to 1 and is linearly proportional to the proportion of shared taxa (Cheetham and Hazel, 1969). Indices were computed separately for species, genera, and families; the three values were averaged to give a composite measure of taxonomic similarity. This procedure diminishes the effect of taking at face value the names and ranks assigned to taxa, particularly for South American groups taxonomic treatments of which have been uneven in scope and quality.

Cluster analyses of assemblages in relation to taxonomic structure were performed on the 1’s complements of similarity values ($D = 1 - S = [N_1 + N_2 - 2N]/[N_1 + N_2]$) using the UPGMA clustering algorithm (Sneath and Sokal, 1973).
Description of Morphology

The biological reliability of any morphological study is critically dependent on how form and form differences are quantified and analyzed (Strauss and Bookstein, 1982; Bookstein et al., 1985). The geometric and statistical methods used in this study were chosen (1) to provide a fairly complete morphological description of each species, unbiased by prior functional expectations; (2) to encompass sets of functionally analogous anatomical reference points (= landmarks); (3) to explicitly include information on ontogenetic (allometric) variation; and (4) to allow forms to be archived and reconstructed.

Species in each assemblage were represented by 5-12 specimens, deliberately chosen to give the largest size range possible (from 1:1.5 to 1:17, smallest:largest standard lengths). All species were used except for several extreme phenotypes: anguillids, synbranchids, gymnotids, and rhamphichthyids. Data consisted entirely of mensural characters (distances measured with respect to anatomical landmarks). Specimens were photographed in lateral aspect, with accompanying metric scale, with the use of small insect-mounting pins to locate midsagittal landmarks (e.g., anus, supraoccipital crest) that could not easily be seen from lateral view. Landmarks (fig. 17.1) were marked on each photograph and digitized as Cartesian coordinates. Euclidean distances were subsequently computed between pairs of scaled landmark coordinates; distances were selected to form ‘‘trusses’’ (fig. 17 1A; Strauss and Bookstein, 1982) and additional combinations of measurements in lateral projection (fig. 17.1B). Auxiliary measurements of body width, taken with digital calipers into a computer file, were used to approximate a triangulation in dorsal projection (fig. 17.1C); bilateral measurements were averaged before analysis. Body-width measurements and distances across the abdomen were selected to be minimally affected by variation in volume of gas bladder, gut, or ovaries. The resulting data set adequately describes the major features of external body form, including body proportions and relative sizes and positions of mouth, eye, head, and fins. It omits information about complex fin shapes; degree of separation of dorsal fins; adipose fins, barbels, and other specialized appendages; and internal anatomy.

Morphological Space

Analyses are based on the positions of specimens in a multidimensional morphological hyperspace (morphospace) the axes of which are logarithms of the 54 mensural characters. The logarithmic transformation linearizes allometries, standardizes variance, and produces a scale-invariant covariance matrix (Bookstein et al., 1985).

Ontogenetic size variation was explicitly included as a major factor by an examination of secondary size-independent patterns of variation with respect to multivariate size factors. This procedure takes into consideration the substantial changes in form that occur during growth. It also negates the necessity of arbitrarily limiting size ranges to ‘‘adults.’’

The full morphospace was reduced by means of principal component analysis (PCA) of the covariance matrix (Bookstein et al., 1985). Use of the covariance matrix preserves allometries and leaves the geometric space undistorted, so that Euclidean distances based on original log measurements and on principal component scores are identical. Because of the large size ranges within and among species, the first component was in all cases a strong size vector, accounting for > 72% of the total variance within assemblages and > 97% of the variance within species, with consistently positive loadings. The first five components always accounted for > 98% of the variance among species; thus the sixth and subsequent components were disregarded for multivariate comparisons (but not for calculation of nearest-neighbor distances). For size-free comparisons among assemblages, sheared principal components (Humphries et al., 1981; Bookstein et al., 1985) were computed by regressing out the pooled within-group size factor (PC1) while maintaining the group centroids. Sheared components are very stable discriminant axes that are unaffected by differences in mean size among groups.

Fig. 17.1. The set of 56 mensural characters used for morphometric analyses. Anatomical landmarks are indicated by open circles; distance measures, by dotted lines. A: Midsagittal truss measures. B: Auxiliary measures in lateral projection. C: Auxiliary measures in dorsal projection.
Assessment of pairwise congruence of morphological variation among assemblages was based on shared principal component analyses. For each pairwise comparison the data for two assemblages were pooled, PCs were extracted, and PC 1 was sheared (regressed) from components 2-5. Within this reduced size-free space, loadings can be represented as vector correlations (directional cosines; Wright, 1954), estimated for each mensural character by its correlations with projection scores across individuals (fig. 17.3). The correlation between assemblages for each character is the cosine of the angle between corresponding vectors. Mean character correlation was estimated by standardizing all character correlations between assemblages with arc sine transformations (Sokal and Rohlf, 1981) and re converting the mean value across characters with an inverse arc sine transformation.

Species-packing analyses were based on PCAs performed separately for each assemblage. Size-independent nearest-neighbor distances (NNDs) were computed within the reduced (n - 1, for n characters) PC space from which the first component had been sheared. Distributions of NNDs were compared against random models using the method of Donnelly (1978) and Sinclair (1985).

Results

Similarity in Faunal Composition Among Assemblages

The two PA and two PY assemblages were initially intended to be pairs of ‘‘replicates’’ sampled from within major drainage basins. The PA samples are similar at all three taxonomic levels (table 17.2), except for the presence of ictalurids and a cyprinodont at Little Fishing Creek and for several substitutions of congeneric species. The Paraguayan assemblages are much less similar to one another than is the PA pair owing to the presence of a diverse collection of catfishes at the Río Paraná locality. The ON, TX, and CA groups share intermediate numbers of taxa at all taxonomic levels. The CA assemblage, which is small and has a high degree of endemism (Moyle and Vondracek, 1985), is the most dissimilar among the North American assemblages. As expected, there is almost no faunal overlap between the Paraguayan and the North American groups; Río Paraná and Little Sandy Creek

<table>
<thead>
<tr>
<th>Locality</th>
<th>1 PA</th>
<th>2 PA</th>
<th>3 ON</th>
<th>4 TX</th>
<th>5 CA</th>
<th>6 PY</th>
<th>7 PY</th>
<th>8 Composite</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. PA</td>
<td></td>
<td></td>
<td></td>
<td>17</td>
<td>12</td>
<td>5</td>
<td>7</td>
<td>6, 7, 8</td>
</tr>
<tr>
<td>2. PA</td>
<td>0.70</td>
<td></td>
<td></td>
<td>5</td>
<td>6</td>
<td>3</td>
<td>2</td>
<td>1, 5, 5, 0, 0, 0, 0, 0, 5, 6, 6</td>
</tr>
<tr>
<td>3. ON</td>
<td>0.52</td>
<td>0.39</td>
<td></td>
<td>3</td>
<td>8</td>
<td>7</td>
<td>0</td>
<td>0, 0, 0, 6, 8, 8</td>
</tr>
<tr>
<td>4. TX</td>
<td>0.57</td>
<td>0.39</td>
<td>0.47</td>
<td></td>
<td>3</td>
<td>8</td>
<td>1</td>
<td>0, 1, 1, 3</td>
</tr>
<tr>
<td>5. CA</td>
<td>0.30</td>
<td>0.64</td>
<td>0.13</td>
<td></td>
<td>20</td>
<td></td>
<td>0</td>
<td>0, 0, 0, 0, 1, 7, 8</td>
</tr>
<tr>
<td>6. PY</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td>0.04</td>
<td>0.00</td>
<td></td>
<td>9, 13, 4, 8, 8, 9</td>
</tr>
<tr>
<td>7. PY</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td></td>
<td>0.00</td>
<td>0.00</td>
<td>0.45</td>
<td>5, 5, 5</td>
</tr>
<tr>
<td>8. Composite</td>
<td>0.37</td>
<td>0.32</td>
<td>0.43</td>
<td>0.31</td>
<td>0.23</td>
<td>0.38</td>
<td>0.27</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 17.2. Dendrograms of assemblages clustered by taxonomic dissimilarity, excluding (A) and including (B) the composite sample. Locality abbreviations are given in table 17.1.
possess a single but different poeciliid each. Dendograms of the assemblages (fig. 17.2) provide an overall assessment of taxonomic similarity.

Congruence of Morphological Distribution

All assemblages overlap considerably in morphological space, and no pairwise combinations of localities could be discriminated (fig. 17.3). However, species are not distributed evenly or randomly within assemblages; observed distributions of nearest-neighbor distances indicate that species are significantly clustered, with NNDs both longer and shorter than expected based on random models.

Comparisons of assemblages in the sheared PC space of fig. 17.3 are meaningful only to the extent that the within-assemblage size vectors (within-group PC 1 axes) are parallel within the full morphological space (Humphries et al., 1981). Pairwise correlations among size vectors are all > 0.90 (table 17.3), indicating that PC 1 as a multivariate measure of body size is highly consistent across species and assemblages.

Mean character vectors within the sheared PC space (fig. 17.3B) characterize the major size-independent trends in body form within and among assemblages. At a given body size species vary from elongated forms (lower right of fig. 17.3B) with relatively wide body, posteriorly displaced medial fins, and wide oral gape, to deep-bodied, narrow forms (upper left). Size of the head and associated cephalic features (snout length, eye diameter, posterior displacement of pectoral fin, etc.) are more or less independent of this morpholine. These and other associated trends are generally consistent with the major shape variations observed by Flanagan (1981) for marine reef fishes. Note that these are average character correlations across all assemblages; as described below, the trends within any particular assemblage deviate from these to some extent.

Patterns of Species Packing

The average morphological “density” of species within assemblages, as indicated by mean nearest-neighbor distance (NND), is not a function of number of species (fig. 17.4A). Species in diverse assemblages are neither more nor less similar than species in depauperate ones. The slight nonsignificant trend of decreasing distance with increasing number in fig. 17.4A is due to the influence of the two Paraguayan assemblages, which have slightly smaller (but not significantly different) mean NNDs from those of the North American assemblages. However, when total occupied morphological space (that is, total size-independent variance subset) is examined as a function of diversity (fig. 17.4B) there is a significant positive relationship, indicating that the total space occupied (total variance) increases in proportion to the number of species present. Again, the Paraguayan species are relatively more similar to one another than are the North American species. For example, the Río Paraná assemblage, with 38 species, has approximately the same total variance as a PA assemblage having 28 species; and the Río Aquidabán, with 24 species, has about the same variance as Lake Opinicon, with only 16 species.

Table 17.3. Pairwise Correlations Among Size Vectors (Within-Assemblage PC 1) (Above Diagonal) and Among Sets of Character Vectors (Below Diagonal)

<table>
<thead>
<tr>
<th>Locality</th>
<th>1 PA</th>
<th>2 PA</th>
<th>3 ON</th>
<th>4 TX</th>
<th>5 CA</th>
<th>6 PY</th>
<th>7 PY</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. PA</td>
<td>—</td>
<td>0.99</td>
<td>0.97</td>
<td>0.96</td>
<td>0.96</td>
<td>0.93</td>
<td>0.93</td>
</tr>
<tr>
<td>2. PA</td>
<td>0.77</td>
<td>—</td>
<td>0.97</td>
<td>0.96</td>
<td>0.96</td>
<td>0.95</td>
<td>0.95</td>
</tr>
<tr>
<td>3. ON</td>
<td>0.44</td>
<td>0.42</td>
<td>—</td>
<td>0.98</td>
<td>0.96</td>
<td>0.94</td>
<td>0.94</td>
</tr>
<tr>
<td>4. TX</td>
<td>0.63</td>
<td>0.49</td>
<td>0.73</td>
<td>—</td>
<td>0.96</td>
<td>0.93</td>
<td>0.93</td>
</tr>
<tr>
<td>5. CA</td>
<td>0.37</td>
<td>0.71</td>
<td>0.28</td>
<td>0.24</td>
<td>—</td>
<td>0.91</td>
<td>0.91</td>
</tr>
<tr>
<td>6. PY</td>
<td>0.32</td>
<td>0.25</td>
<td>0.19</td>
<td>0.20</td>
<td>0.07</td>
<td>—</td>
<td>0.98</td>
</tr>
<tr>
<td>7. PY</td>
<td>0.28</td>
<td>0.17</td>
<td>0.16</td>
<td>0.34</td>
<td>0.26</td>
<td>0.44</td>
<td>—</td>
</tr>
</tbody>
</table>
The Importance of Phylogenetic Constraints in Comparisons of Morphological Structure

Distributions of NNDs are significantly nonrandom ($P << 0.01$) for all assemblages and indicate clustering within morphospace with respect to random models. This nonrandomness could be due to phylogenetic patterning, in that confamilial and congeneric species might be expected to aggregate and to be distant from less closely related species (Gatz, 1979a). To examine this possibility, NND distributions were determined for cyprinids in the two PA assemblages and for characids in the two PY assemblages; of the families studied, these were the only ones having sufficient numbers of species for comparison. In all four cases NND distributions were not significantly different from random (though somewhat overdispersed), indicating that the morphospace aggregations do correspond to taxonomic groupings at the family level.

Congruence of Morphological Structure

Mean character correlations, estimated among all possible pairs of assemblages (table 17.3), range from 0.77 between the two PA localities to a nonsignificant 0.07 between the CA and Río Paraná (PY) assemblages. The high congruence between the PA “replicates” is not surprising; if two such localities had exactly the same species composition, their patterns of morphological variation should be identical except for minor differences owing to geographic variation. However, there is no prior expectation for correlations between North American and South American assemblages, which actually range from 0.07 (CA-PY) to 0.34 (TX-PY) with a mean correlation of 0.20. Such low correlations seem to indicate that phylogenetic differences among component species are more important than ecological constraints in determining overall patterns of morphological structure.

Moreover, the effect of taxonomic similarity is clinal rather than discrete. The linear relationship between mean character correlation and taxonomic similarity (fig. 17.5) is highly significant ($r = 0.82, t = 7.3, df = 26, P << 0.01$). Thus assemblages having intermediate levels of taxonomic similarity are also intermediate in morphological congruence. The regression function, when extrapolated to the case of identical faunal composition ($S = 1$), gives a pre-

Fig. 17.4. Scatterplots of (A) mean nearest-neighbor distances and (B) total size-independent morphological variance as functions of number of species within each assemblage. Variance is expressed as a percentage of total size-independent variance among all assemblages. Solid circles = North American localities; open circles = South American localities. The expected grand-mean NND for randomly distributed points would be 0.51; observed values are significantly less than expected, indicating aggregation.

Fig. 17.5. Scatterplot of morphological congruence as a function of taxonomic similarity for all pairs of assemblages, including the composite. Each point represents one assemblage pair. The regression line assumes independent residuals; observed residual correlations were statistically negligible.
predicted mean character correlation not significantly different from the expected 1. The predicted mean correlation of 0.20 for complete taxonomic dissimilarity is a measure of the amount of congruence expected from ecological constraints acting alone.

**Discussion**

Morphological approaches to descriptive analyses of community relationships are based on the premise that morphological features of organisms reflect in large part their ecological relationships, or at least that morphological analyses may reveal patterns of structure that require explanation in the context of ecological and evolutionary theory (Ricklefs and Travis, 1980; Douglas, chap. 18). The concept of morphological structure within a community or assemblage has had a dual context in the literature, being used in some cases to indicate the spatial patterns of species within the morphospace, particularly in terms of distances between species and overlap among groups of species, and in other cases to indicate patterns of variation among morphological characters. Because convergence in body form and other features seems to be widespread among fishes in both freshwater and marine habitats (at least at a gross morphological level), it might seem likely that the ecological interactions that sort out coexisting combinations of species may structure assemblages in predictable ways, even if a one-for-one replacement of species in different habitats does not occur (Schlosser, 1982a).

The results of this study, however, suggest that the ability to predict patterns of variation among communities is limited by the degree to which the component species have been derived from a common evolutionary and biogeographic background. Thus a serious methodological problem concerns the scale of sampling. Population sizes and degrees of ecological overlap among species may vary widely both spatially and temporally, and the detection of repeatable patterns may be a critical function of the scale on which ecological processes act, particularly in relation to magnitudes of gene flow among populations inhabiting different communities and experiencing varying combinations of predators, prey, competitors, and physical-habitat characteristics. Nevertheless, these results should serve as a caveat for the comparative study of ecomorphological patterns. When the communities chosen for study lie within the same biogeographic or faunal region, a high degree of concordance is to be expected (e.g., Gatz, 1979a, 1981).

Schoener (1974) originally suggested that the total amount of "niche space" occupied by an assemblage of coexisting species should enlarge as the number of extant species increases, because additional species may utilize previously unused aspects of the available ecological resources. This hypothesis has been tested indirectly by a number of investigators using morphological analysis (e.g., Karr and James, 1975; Findley, 1973, 1976; Ricklefs and O'Rourke, 1975; Gatz, 1979a; Ricklefs and Travis, 1980; Ricklefs et al., 1981; Findley and Black, 1983). Their results, and those of this study, have generally supported Schoener's hypothesis that the "core" of the community space, consisting of relatively unspecialized species, is ecologically saturated and that species are added to a community in secondary or novel directions. An alternative explanation is that the ecological conditions of less diverse communities are favorable only to generalist species (Ricklefs and Travis, 1980); however, the continuous relationship between total morphological variance and species number, demonstrated in this study, would argue against a hypothesis invoking response to harsh or variable environments as a general controlling mechanism. A possible mechanism for the assemblage of freshwater fishes into specific habitats is the sorting out from the regional source pool of species (both specialized and unspecialized) that can coexist in the short term, with minor subsequent modification following from competitive ecological interaction.

These findings are complementary to those of Mayden (chap. 26) in demonstrating that an understanding of the history of a community is an important prerequisite to assessing the degree to which morphological features have been molded by competition or other ecological interactions (see also Brooks, 1985). In the absence of detailed knowledge about the phylogenetic relationships of component taxa and the geological history of the regions under study, it is impossible to judge the extent to which extant communities have resulted from recent coevolutionary processes versus the chance assemblage of historically available species. In such cases assessment of faunal similarity will at least provide a rough estimate of the amount of morphological congruence expected among assemblages in the absence of adaptive modifications.

In summary, the hydrodynamic and competitive constraints imposed by the aquatic environment do not necessarily lead to morphological similarity among assemblages by way of evolutionary convergence, at least with regard to patterns of variation among species. The teleost "morphotype" seems to be sufficiently flexible that morphological structure need not be highly constrained in similar ways in different habitats. Instead, each characteristic body form exploits the aquatic environment somewhat differently in terms of its own morphological and ecological design, and resultant differences among species (in magnitude and direction) are highly variable. Thus phylogenetic patterns of form diversity are responsible both for consistency among different fish assemblages within the same biogeographic regions and for noncongruence among assemblages having little faunal similarity.¹

¹The University of Michigan Morphometrics Study Group served as the forum in which much of my philosophy about biological form and geometric morphometry was developed, and I am grateful to the participants: F. L. Bookstein, B. Chernoff, R. L. Elder, J. M. Humphries, and G. R. Smith. I thank E. L. Cooper for use of the PSU collections, and R. R. Miller, G. R. Smith, and W. L. Fink for use of the UMMZ collections. Critical comments by M. E. Douglas, M. A. Houck, and G. D. Schnell substantially improved the manuscript. National Science Foundation grant BSR-8307719 provided financial support.
LITERATURE CITED


