Metamorphic Growth-Gradient Changes in South American Loricariiid Catfishes *Loricariichthys maculatus* and *Pseudohemiodon laticeps*

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Studies on Neotropical Fauna and Environment 30, pp. 177-191.

Metamorphosis is of particular interest in ecological and evolutionary studies because the decoupling of larval and adult growth patterns potentially allows the adaptive diversification of the separate stages. To better understand how differential growth patterns might contribute to evolutionary differences in body form, growth allometries in relation to interspecific morphometric differences were studied in two species of loricariid catfishes that can be completely discriminated in the smallest larvae examined. Many characters undergo metamorphic shifts in allometric growth rates, although the timing of the shifts seems to vary among characters. Interspecific allometric differences are highly correlated with the discriminatory values of the characters in larvae, but a comparable correlation is absent in adults. This suggests that metamorphosis serves to "release" adult growth patterns from phylogenetic constraints on growth.

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**Introduction**

Studies of morphological development have contributed significantly to our understanding of the evolution of form and function in vertebrates (Lauder, 1981; Liem & Wake, 1985). In particular, ontogenetic studies have focused attention on the relationships between allometric scaling, function, and ecological role. But despite numerous quantitative studies of vertebrates that exhibit continuous, relatively smooth changes in form during growth, relatively little is known about patterns of growth gradients in vertebrate species that undergo relatively rapid changes in morphology. Metamorphic species are of particular interest because of the complexity and rapidity of concurrent changes that take place in both form and function, and because of the decoupling of larval and adult growth patterns that can occur across metamorphosis (Shaffer & Lauder, 1988; Harris, 1989; Nodzenski & Inger, 1990). Although not as rapid or dramatic as amphibian metamorphoses, the growth patterns of many fishes are known to change rapidly during the larval and early juvenile stages of development (Mar-
tin, 1949; Gihr, 1957; Fuiman, 1983; Strauss & Fuiman, 1985; Strauss, 1992). Such decouplings of life stages can potentially allow an adaptive fine-tuning of morphology in the separate stages that might be much more constrained were allometric relationships constant throughout ontogeny.

An adequate assessment of morphological change during growth must be based on a comparison of growth patterns between larvae, juveniles, and adults. Growth patterns are difficult to assess with precision unless the specimens available for study represent a significantly large range in body size. This usually entails culturing and spawning the fishes in the laboratory, hatching the egg masses, and successfully raising the young and preserving representative samples across time. However, for many species these tasks require critical information about the ecological requirements of each species, and even when such lab-raised specimens are available the effects of the artificial aquarium conditions on growth patterns must be assessed by comparison with individuals from natural populations.

For this study I have utilized published morphometric data for samples of freshly collected adults and newly hatched fry of two species of loricariid catfishes, *Loricariichthys maculatus* (Machado Allison & López Rojas, 1975) and *Pseudoheemiiodon laticeps* (López Rojas & Machado Allison, 1975). The study had three objectives: (1) to characterize the allometric patterns of growth in these species by providing statistical estimates for the growth allometries of each of the mensural traits, and to determine how allometric growth rates differ between life stages and between species; (2) to describe the primary size-independent differences in growth and form; and (3) to determine the extent to which differential growth patterns account for the observed differences in body form.

**Materials and Methods**

**Study Organisms**

Data were available on 39 specimens of *Loricariichthys maculatus* (identified by them as *L. typus*) collected from the Río Portuguesa (tributary of the Río Apure, Orinoco drainage) at Camaguan, Estado Guárico, Venezuela (Machado Allison & López Rojas, 1975). A number of adult specimens were found to be incubating egg masses in their buccal cavities, from which larvae and juveniles up to 60 days of age were obtained. Measurements (in mm) of 18 mensural characters were provided for the 39 adults (91.5-189.0 mm standard length) and 9 larvae (8.6-12.0 mm); incomplete data, for 13 of the 18 characters, were given for an additional 15 larvae (6.7-10.8 mm). I have used 14 of the 18 characters (see below) in the present study; those labelled LEB, LPR, ACA, and LAC in Tables 1 and 2 of Machado Allison & López Rojas (1975) were omitted because they were insufficiently described. Five meristic counts were also provided for all specimens, but were invariant and thus ignored.

Data were available for 9 adults of *Pseudoheemiiodon laticeps* (identified by them as *Loricaria laticeps*) collected from the Río Boconó (tributary of the Río Guanare, Orinoco drainage), Estado Portuguesa, Venezuela (López Rojas & Machado Allison, 1975). Several specimens of these were carrying eggs in their buccal cavities, from which larvae of up to 24 hrs of age were obtained. Measure-
ments of 13 characters were detailed in their Table 3, 12 of which were consistent with those for \textit{Loricariichthys maculatus}. Two sets of data were given for larvae: one set of character means for three newly hatched larvae (mean standard length = 16.0 mm), and one set of means for 10 larvae that died after 24 hr (mean length = 16.5 mm). I tentatively categorized two other individuals (26.7 and 37.0 mm) as “larvae” to allow an assessment of early growth trends. Adults ranged from 104.5 mm to 208.3 mm standard length. Meristic data were invariant.

**Mensural Characters**

Many of the characters were measured as the distance from the snout to a fin or other anatomical structure. In order to better describe regional body growth and reduce redundancy (Strauss & Bookstein, 1982), two such characters were converted to differences between the character as measured and another character highly redundant with the first: caudal length (CL) was estimated as the difference between standard length (SL) and total length (TL), and abdomen length (AL) was estimated as preanal length (PAL) minus prepelvic length (PVL). Because the morphometric data for both species were collected by the same researchers, artifactual variation due to differences in technique has been largely avoided. The characters used in this study are based on those illustrated in López Rojas & Machado Allison (1975 : 62). They are described here along with their assigned mnemonic abbreviations:

1. SL – standard length, from snout to end of vertebral column (hypural plate);
2. HL – head length, from tip of snout to posterior edge of supraoccipital crest;
3. HW – maximum head width;
4. MBL – length of maxillary barbel;
5. SNL – snout length, from tip of snout to nearest edge of orbit;
6. OD – orbit diameter parallel to the longitudinal body axis;
7. IOW – least interorbital width (\textit{L. maculatus} only);
8. PDL – predorsal length, from tip of snout to dorsal-fin spine;
9. PPL – prepectoral length, from tip of snout to anterior base of pectoral fin (\textit{L. maculatus} only);
10. PVL – prepelvic (prevertical) length, from tip of snout to anterior base of pelvic fins;
11. AL – abdomen length, the difference between PVL and preanal length (PAL) as measured from tip of snout to anal-fin spine;
12. CPL – caudal-peduncle length, from base of the posterior anal-fin ray to end of vertebral column;
13. CPD – least caudal-peduncle depth;
14. CL – caudal-fin length (excluding caudal filament), the difference between SL and total length (TL).

**Methods of Analysis**

For multivariate analyses, all measurements were converted to natural logarithms. The logarithmic transformation has several beneficial effects on the data structure: for individual characters, the variances become independent of their mean values (and thus comparable to one another in terms of intrinsic variability) to the extent that the individual coefficients of variation are constant (Lewontin, 1966; Lande, 1977); among characters, exponential bivariate and multivariate...
allometric relationships become colinear, with slopes that characterize relative growth rates with respect to body size (Bookstein et al., 1985; Strauss, 1993). A general size factor was estimated separately for each species as the first principal component (PC1) of the within-group covariance matrix (Jolicoeur, 1963). Because the first principal component (PC1) of these data is a strong size factor (accounting for more than 99% of the total variation in each sample), the position (score) of an individual on PC1 is a measure of its general body size (Bookstein et al., 1985; Strauss, 1987). In using PC1 as a measure of general size, size is implicitly defined to be that linear combination of characters that best accounts for the joint increase in all characters simultaneously, in the sense of leaving the smallest mean square residual. In order to make the size factors for the two species directly comparable, only the 12 characters in common were used to compute PC1 (omitting IOW and PPL for *P. laticeps*).

Relative growth rates of each character with respect to change in general body size initially were examined using the moving-regression procedure of Forbes & Lopez (1989), and many were observed to shift significantly during growth. Thus allometric shifts were measured on a character-by-character basis in the context of a two-stage bilinear spline model (Figs. 1, 2), fitted to the data by regression (Hudson, 1966; Brooks, 1991; Strauss, 1992). Using a quasi-Newton optimization method (Shanno, 1970), the inflection point for each regression was allowed to vary within the range of data to maximize the variance explained by the model. The statistical significance of the bilinear model was assessed in relation to the standard linear allometric model. Because the bilinear model has two more parameters than the linear model, it will always provide at least as good a fit (i.e., explain at least as much variance); therefore its significance was estimated using an F-statistic (Neter et al., 1985: 94-96; Brooks, 1991; Strauss, 1992) that measures the relative improvement of fit in relation to the number of additional parameters.

The slopes of the two segments for each character with respect to general size were used as estimates of its ‘larval’ and ‘adult’ allometric coefficients, which were rescaled within species to a mean of 1.0. Such multivariate allometries are estimates of the relative rates of change (i.e., growth rates) of individual characters with general size, a robust measure of biological age (Leamy & Bradley, 1982; Strauss, 1987). Thus, an allometric coefficient of exactly 1.0 implies isometry (unit change in the character for a unit in body size), coefficients significantly greater than unity describe positive allometry (a relative increase in the character with increase in size), and those significantly less than unity indicate negative allometry (relative decrease in the character with size). Characters were judged to be isometric (the null hypothesis) when they were neither significantly positively nor negatively allometric, based on standard errors of the slopes. If an organism were growing isometrically (a rare condition), it would not change its body shape during growth. Allometrically growing organisms alter their body proportions as they become larger. It should be noted that, because these allometric coefficients are derived from samples of individuals each measured once, they might not strictly represent patterns of individual growth (Cock, 1966). However, the patterns of multivariate allometry do account very well for intraspecific variation in shape.

Morphometric differences between species independent of allometric variation in body sizes were assessed by size-invariant discriminant analysis (dos Reis
Fig. 1. Scatter plots and fitted bilinear functions of selected characters (logarithmic axes) versus general body size (within-group PCI) for larvae and adults of *Loricariichthys maculatus*. Inflection points are indicated by solid square points.
Fig. 2. Scatter plots and fitted bilinear functions of selected characters (logarithmic axes) versus general body size (within-group PCI) for larvae and adults of *Pseudohemiodon laticeps*. Inflection points are indicated by solid square points.
et al., 1990). Discrimination coefficients (loadings) were rescaled as vector correlations of characters with the discriminant function (Strauss, 1985).

Standard errors for allometric coefficients, inflection points, and discriminant-function loadings were obtained by bootstrapping (Efron & Tibshirani, 1986; Noreen, 1989). Each analysis was bootstrapped with 1000 random subsamplings of the data, accumulating sampling distributions of the relevant statistics. Symmetric standard errors were calculated as the standard deviations of the corresponding sampling distributions (Hall, 1988).

All computations were performed using version 3.5m of 386-MATLAB (Mathworks, 1991, 1992) on a Compaq Deskpro 50M personal computer. Copies of specialized MATLAB functions written to fit and to bootstrap two-stage allometric trajectories and size-invariant discriminant analyses are available from the author.

Results

Allometric Growth in Larvae and Adults
Multivariate growth allometries were calculated with respect to general “size factors”, estimated separately for each species by the first principal component (PC1) of the log-transformed morphometric data. Because body length ranged from 8.6-189.0 mm standard length (SL) in Loricariichthys maculatus and 16.0-208.3 mm SL in Pseudohemiodon laticeps, the size factors accounted for very large proportions of the total variance in each sample: 99.4% in L. maculatus and 99.5% in P. laticeps.

In general, growth allometries may be quite different for larvae and adults (Fig. 3; Tables 1,2) because relative growth rates of different body regions change

![Graphs](https://www.example.com/graph.png)

Fig. 3. Changes in multivariate growth patterns across the transformation from larval to adult body form for the two loricariid species. Each character is represented by a line connecting the allometric coefficients (relative growth rates) of the larval and adult stages, respectively. See text for character mnemonics.
Table 1. Multivariate allometric coefficients (+ estimated standard errors) for mensural characters of *Loricariichthys maculatus*. The inflection point is the standard length at which the shift in relative growth rate is predicted to occur, based on the fitted bilinear model.

<table>
<thead>
<tr>
<th>Character</th>
<th>Larvae (N=25)</th>
<th>Adults (N=39)</th>
<th>Pooled (N=64)</th>
<th>Inflection Point</th>
<th>Binlinear Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length</td>
<td>0.95 ± 0.09</td>
<td>1.07 ± 0.04</td>
<td>1.05 ± 0.01</td>
<td>13.2 ± 10.3</td>
<td>6.26 0.007*</td>
</tr>
<tr>
<td>Head length</td>
<td>1.01 ± 0.17</td>
<td>0.95 ± 0.04</td>
<td>0.98 ± 0.01</td>
<td>33.5 ± 20.7</td>
<td>0.19 1.000</td>
</tr>
<tr>
<td>Head width</td>
<td>0.36 ± 0.08</td>
<td>1.07 ± 0.02</td>
<td>0.93 ± 0.01</td>
<td>15.6 ± 1.3</td>
<td>124.58 &lt;0.001*</td>
</tr>
<tr>
<td>Barbel length</td>
<td>1.33 ± 0.13</td>
<td>0.98 ± 0.04</td>
<td>1.04 ± 0.01</td>
<td>13.2 ± 6.5</td>
<td>8.94 &lt;0.001*</td>
</tr>
<tr>
<td>Snout length</td>
<td>1.83 ± 0.17</td>
<td>1.02 ± 0.02</td>
<td>1.23 ± 0.01</td>
<td>18.3 ± 2.7</td>
<td>16.42 &lt;0.001*</td>
</tr>
<tr>
<td>Orbit diameter</td>
<td>0.67 ± 0.13</td>
<td>0.72 ± 0.09</td>
<td>0.68 ± 0.01</td>
<td>88.8 ± 78.2</td>
<td>0.38 1.000</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>0.92 ± 0.12</td>
<td>1.04 ± 0.06</td>
<td>0.99 ± 0.01</td>
<td>31.5 ± 24.3</td>
<td>0.23 1.000</td>
</tr>
<tr>
<td>Predorsal length</td>
<td>0.93 ± 0.04</td>
<td>1.07 ± 0.05</td>
<td>1.00 ± 0.01</td>
<td>30.3 ± 12.5</td>
<td>1.23 0.597</td>
</tr>
<tr>
<td>Prepectoral length</td>
<td>0.90 ± 0.07</td>
<td>1.00 ± 0.30</td>
<td>0.98 ± 0.01</td>
<td>13.2 ± 6.7</td>
<td>0.94 0.793</td>
</tr>
<tr>
<td>Prepelvic length</td>
<td>0.53 ± 0.12</td>
<td>1.05 ± 0.02</td>
<td>0.98 ± 0.01</td>
<td>13.3 ± 0.9</td>
<td>25.62 &lt;0.001*</td>
</tr>
<tr>
<td>Abdomen length</td>
<td>1.72 ± 0.43</td>
<td>1.03 ± 0.04</td>
<td>1.19 ± 0.02</td>
<td>16.9 ± 12.6</td>
<td>3.22 0.094</td>
</tr>
<tr>
<td>Caudal-peduncle length</td>
<td>1.00 ± 0.12</td>
<td>1.21 ± 0.07</td>
<td>1.11 ± 0.01</td>
<td>28.7 ± 17.1</td>
<td>0.31 1.000</td>
</tr>
<tr>
<td>Caudal-peduncle depth</td>
<td>0.22 ± 0.23</td>
<td>1.09 ± 0.04</td>
<td>0.77 ± 0.01</td>
<td>24.1 ± 5.0</td>
<td>22.00 &lt;0.001*</td>
</tr>
<tr>
<td>Caudal-fin length</td>
<td>1.19 ± 0.15</td>
<td>1.07 ± 0.10</td>
<td>1.09 ± 0.01</td>
<td>13.3 ± 12.8</td>
<td>1.32 0.547</td>
</tr>
</tbody>
</table>

Table 2. Multivariate allometric coefficients (± estimated standard errors) for mensural characters of *Pseudohemiobodon laticeps*. The inflection point is the standard length at which the shift in relative growth rate is predicted to occur, based on the fitted bilinear model.

<table>
<thead>
<tr>
<th>Character</th>
<th>Larvae (N=4)</th>
<th>Adults (N=7)</th>
<th>Pooled (N=11)</th>
<th>Inflection Point</th>
<th>Binlinear Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length</td>
<td>0.87 ± 0.15</td>
<td>1.06 ± 0.09</td>
<td>1.00 ± 0.02</td>
<td>39.4 ± 9.4</td>
<td>1.74 0.489</td>
</tr>
<tr>
<td>Head length</td>
<td>1.11 ± 0.16</td>
<td>1.14 ± 0.07</td>
<td>1.14 ± 0.02</td>
<td>40.0 ± 19.8</td>
<td>0.21 1.000</td>
</tr>
<tr>
<td>Head width</td>
<td>0.96 ± 0.04</td>
<td>1.09 ± 0.11</td>
<td>1.00 ± 0.01</td>
<td>95.1 ± 32.9</td>
<td>4.16 0.129</td>
</tr>
<tr>
<td>Barbel length</td>
<td>1.65 ± 0.28</td>
<td>0.98 ± 0.09</td>
<td>1.20 ± 0.06</td>
<td>40.9 ± 7.3</td>
<td>4.24 0.125</td>
</tr>
<tr>
<td>Snout length</td>
<td>1.29 ± 0.10</td>
<td>1.09 ± 0.06</td>
<td>1.15 ± 0.02</td>
<td>39.4 ± 15.1</td>
<td>2.32 0.337</td>
</tr>
<tr>
<td>Orbit diameter</td>
<td>0.57 ± 0.55</td>
<td>0.70 ± 0.39</td>
<td>0.63 ± 0.03</td>
<td>77.1 ± 44.3</td>
<td>0.05 1.000</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Predorsal length</td>
<td>0.82 ± 0.06</td>
<td>1.03 ± 0.02</td>
<td>0.96 ± 0.02</td>
<td>42.9 ± 9.4</td>
<td>22.64 0.002*</td>
</tr>
<tr>
<td>Prepectoral length</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Prepelvic length</td>
<td>0.84 ± 0.08</td>
<td>1.18 ± 0.06</td>
<td>1.00 ± 0.02</td>
<td>63.5 ± 19.1</td>
<td>16.39 0.005*</td>
</tr>
<tr>
<td>Abdomen length</td>
<td>1.18 ± 0.08</td>
<td>0.92 ± 0.08</td>
<td>1.03 ± 0.02</td>
<td>50.9 ± 17.2</td>
<td>2.78 0.258</td>
</tr>
<tr>
<td>Caudal-peduncle length</td>
<td>0.91 ± 0.17</td>
<td>1.15 ± 0.03</td>
<td>1.07 ± 0.03</td>
<td>39.4 ± 7.7</td>
<td>3.10 0.218</td>
</tr>
<tr>
<td>Caudal-peduncle depth</td>
<td>0.73 ± 0.13</td>
<td>0.86 ± 0.12</td>
<td>0.79 ± 0.02</td>
<td>76.8 ± 39.1</td>
<td>0.11 1.000</td>
</tr>
<tr>
<td>Caudal-fin length</td>
<td>0.97 ± 0.09</td>
<td>1.11 ± 0.10</td>
<td>1.03 ± 0.02</td>
<td>61.5 ± 23.1</td>
<td>0.20 1.000</td>
</tr>
</tbody>
</table>

with respect to one another at some time during ontogeny. This is particularly evident for *L. maculatus*, for which the sample sizes are adequate for statistical testing. As in other fishes having reasonably distinguishable larval forms, the shift from larval patterns of growth to adult patterns may take place gradually and at different times in different parts of the body. For any particular character, the body size at which the shift takes place can be estimated by extrapolating larval and adult allometric trends to the intermediate size at which they intersect.
(Figs. 1, 2; Tables 1, 2). As expected, inflection points can be estimated with precision only when larval and adult allometries are significantly different. But even when such trends are well defined, extrapolated points of intersection vary widely among characters. For the six characters that have significantly different intersecting trends in *L. maculatus*, the mean standard length at inflection is 16.3 ± 5.5 mm (Table 1). Few characters exhibit significantly different allometries between larvae and adults of *P. laticeps* because of the small sample size (Table 2), but for the three most significant characters (PDL, PPL, and MBL) the predicted mean length at inflection is 49.1 ± 13.0 mm SL. Until the nature of growth throughout ontogeny is studied in detail in these species, we may consider these to be tentative mean sizes at which larval ‘transformation’ occurs. It is notable that the predicted size at transformation of *P. laticeps* is about three times greater than that of *L. maculatus*.

Within either larvae or adults, allometries can vary considerably among characters (Figs. 1-3). In *L. maculatus*, for example, the smallest larval coefficient is 0.22 for caudal-peduncle depth, which is not significantly different from the case of no growth (no change in peduncle depth with age). The largest is 1.83 for snout length, a more than three-fold increase for every doubling in general body size. Most character allometries become more nearly isometric in adults after transformation. The primary exception in both species is orbital diameter, for which the relative increase in length with growth remains as low in adults as in larvae.

One possible measure of heterogeneity of development is the standard deviation of allometric coefficients among characters. In both species the heterogeneity of allometries is much greater among larval traits than among adult traits (0.46 vs 0.11 in *L. maculatus*, and 0.29 vs 0.14 in *P. laticeps*). Although this may be artifactual in part due to relatively greater measurement errors in very small specimens, the tightness of the larval clusters in the plots of Figs. 1,2 (and corresponding low standard errors of coefficients; Tables 1,2) indicates that the greater heterogeneity (stronger growth gradients) observed in larvae is probably a real phenomenon. That is, larvae change their body forms much more rapidly with a unit increase in body size than do adults.

**Correlations of Allometries Between Stages and Species**

Current hypotheses about the relationships between development and evolution propose that larval growth patterns are more highly conserved phylogenetically than are juvenile and adult patterns. To the extent that this is true in loricariids, the sets of larval allometries of *L. maculatus* and *P. laticeps* should be more highly correlated with one another than are the adult allometries.

Figure 4 shows the results of such comparisons. Neither set of larval allometries is significantly correlated with the corresponding set of adult allometries (Fig. 4A,B), suggesting that larval growth patterns are “uncoupled” with adult patterns via metamorphosis. For *L. maculatus*, the rank correlation across characters is a nonsignificant -0.15; for *P. laticeps*, it is 0.24. Nor are the sets of adult allometries significantly correlated between species \( r = 0.22 \). However, the sets of larval allometries are significantly correlated between species \( r = 0.83, p = 0.001 \), indicating that characters that are highly allometric (either positively or negatively) in one species tend on average to be similarly allometric in the other species.
Fig. 4. Comparisons of allometries among larval and adult stages of the two loricariid species; \( r \) is the Spearman rank correlation, and \( p \) its significance level. Error bars enclose \( \pm 1 \) standard error. Dotted lines are linear regressions. (A, B) Comparisons of larval and adult allometries separately for the two species. (C, D) Comparisons of the two species separately for larval and adult allometries.

Morphological Differences Between Species
Body forms of the two species, as indicated by the 12 mensural characters, are very similar despite the several discrete differences that exist between the genera (Boeseman, 1972, 1976). However, the minor quantitative differences between them are described by a size-invariant discriminant function (DF1 in Fig. 5); because this is a two-group analysis, the second function (DF2) describes only within-group variation. The discriminant function indicates that, at a given body size, _L. maculatus_ is relatively longer, particularly in the snout region, while _P. laticeps_ has a wider head and eye, longer maxillary barbel, and more posteriorly placed pelvic fins.
**Fig. 5.** Size-invariant discriminant analysis of the two loricariid species. Left panel: scatterplot of the two samples on the first two discriminant functions, of which only the first reflects discrimination between species. Right panel: loadings (correlations) of characters on DF1.

**A. Larval allometries**

\[ r = 0.69 \]
\[ p = 0.013 \]

**B. Adult allometries**

\[ r = 0.16 \]
\[ p = 0.62 \]

**Fig. 6.** Correlations of the discriminant-function loadings from Fig. 5 with the differences between corresponding allometric coefficients for the two loricariid species. (A) Larval allometries. (B) Adult allometries.

**Congruence of Allometric and Shape Differences**

Conceptually, it is self-evident that interspecific differences in relative size and shape of homologous structures result from differences in developmental patterns. However, it is unclear whether size-independent differences at this level of taxonomic distinction should be a product only of allometric growth patterns at this stage, or whether the major body-form differences are determined earlier during ontogeny (Strauss, 1992; Strauss & Altit, 1992). One way of approaching
this question is to determine whether the characters found to be most discrimina-
tory are also those for which the allometric coefficients are most different be-
tween species.

Differences between allometries were calculated by subtracting coefficients of \textit{P. laticeps} from corresponding coefficients of \textit{L. maculatus}; the differences were correlated with loadings from the discriminant function (Fig. 6). Although there is no relationship between discriminant loadings and allometric differences in adults (Fig. 6B), the rank correlation for larvae is a highly significant 0.69 ($p = 0.013$); the parametric correlation is an even higher $r = 0.73$ ($p = 0.004$).

**Discussion**

The dynamic aspects of morphogenesis and development provide a high degree of regularity and coordination of the relative growth rates of different parts of the body (Moss, 1968; Hanken, 1983). Such regularities are observable at the phenotypic level as allometric patterns of covariation among morphometric traits (Strauss, 1993), which strongly reflect developmental properties such as contiguity and ontogenetic homology as well as the underlying patterns of genetic covariance (Lande, 1985). Because of the cascading effects of development, in which the growth processes at one stage work on the morphological products of preceding stages, functionally adaptive differences that are selected at later stages of develop-
ment (e.g., juveniles and adults) must be mediated by coordinated changes in growth patterns at earlier stages. Developmental mechanisms that alter patterns of allometric growth (e.g., differential sizes of germinal centers and rates of cell division; Katz, 1980) may permit such adaptive differences in body form to be attained with minimal genetic change (Alberch, 1980; Gould, 1966, 1980).

This study has produced several basic conclusions about altered patterns of growth and differentiation in the loricariid catfishes \textit{Loricariichthys maculatus} and \textit{Pseudohemiodon laticeps}. First, the growth patterns of both species are significantly allometric, indicating systematic changes in body form during growth, but the particular patterns of allometric growth differ in detail between species. The growth patterns are relatively more extreme in larvae and more isometric in adults.

Second, despite these differences in detail, there is a fundamental concordance between the larval patterns, in that characters that are significantly allometric (positively or negatively) in one species tend to be similarly allometric in the other. This concordance is not present in adults. This finding is significant for comparative studies: given the larval allometries of one species, it is possible to predict the larval allometries of a related species with more reliability than it is to predict the adult allometries of the same species.

Third, the two species are distinctive in their body forms and can easily be discriminated morphometrically. Because the species represent different genera, this is not necessarily surprising. However, such differences are observable in even the smallest larvae examined, at a stage just after hatching.

Fourth and most important, the differences that distinguish the species at this intergeneric level seem to be a function of differential growth patterns in larvae, but not in juveniles and adults. In principle, knowing the differences between
relative growth rates should thus allow us to predict morphological differences between species, even though those differences must also be a function of the less extreme (more isometric) growth patterns of post-larval growth.

The possibility exists that these observed metamorphic patterns are atypical for loricariid catfishes because *L. maculatus* and *P. laticeps* are mouth-brooders (as are at least some other loricarian species; Regan, 1904; Menezes, 1949; Lowe-McConnell, 1964, 1975; Isbrücker, 1971; Machado Allison & López Rojas, 1975; Isbrücker & Nijssen, 1979; Moodie & Power, 1982; Taylor, 1983), thus buffering the developing larvae from the external environment within the body of the brooding female. A test of this hypothesis would be provided by parallel studies of ontogenetic patterns of allometric growth gradients in nonbrooding sister taxa of the loricariines (the Hypostominae/Ancistrinae; Schaefer, 1987).

The loricariid catfishes comprise a highly diverse, monophyletic group of fishes distributed throughout South America from the La Plata drainage to Panama. This study is very preliminary because only two species have been studied in detail. Additional contrasts are needed, including comparisons among sister taxa differing in their ecology as well as among species having similar ecomorphological roles but different phylogenetic histories. Because of the extreme diversity of loricariids (more than 600 species in 70 genera, nearly 24% of all described catfishes; Schaefer, 1987), knowledge about their growth patterns will obviously permit a more refined understanding of the ecomorphological requirements and similarities of these fishes.

References


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