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A MULTIVARIATE COMPARISON OF ALLOMETRIC GROWTH PATTERNS

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Abstract.—Multivariate methods for "size correction," such as shearing or multiple-group principal component analysis, assume that the groups under consideration share a common allometric growth pattern. However, this assumption has rarely been tested empirically. A variety of patterns of allometric growth in larvae of 17 species of marine fishes is revealed by principal component analysis. The bootstrap technique is used to assess statistical accuracy, and the hypothesis of one common growth pattern is clearly rejected. Even taxonomically related species are not always similar in their growth patterns. This indicates that techniques for "size correction" should not be applied without testing the assumption of a common growth pattern. To summarize the variation in allometric patterns, a recent approach, principal points, is used to find a small number of "typical" patterns. Flury (1990, Biometrika 77:33–41) defined the k principal points of a multivariate random vector **X** as those points that minimize the expected Euclidean distance of **X** from the nearest principal point. For our data set, four typical allometric patterns are thus characterized by means of principal points. Some common features of allometric patterns are possibly of functional importance, but combinations of different allometric patterns and initial morphologies can lead to a variety of body forms in fish larvae. [Allometric growth; morphometrics; principal component analysis; size correction; principal points; bootstrap.]

Morphometric studies commonly characterize multivariate patterns of allometric growth as the first principal components of within-group covariance matrices (Jolicoeur, 1963). Comparisons of allometric patterns often reveal fairly close similarities between groups of animals, such as different geographical populations (e.g., Gibson et al., 1984; Voss et al., 1990) or ecological variants (e.g., Meyer, 1990) of one species or several related species (e.g., Boitard et al., 1982; Shea, 1985; Creighton and Strauss, 1986; Klingenberg and Zimmermann, in press).

A number of procedures for separating variability in "size" (ontogenetic stage) within groups from variation between groups have been devised. These procedures are based on the assumption that the groups under consideration share a common growth pattern, and most of these methods use the pooled within-group covariance matrix to estimate this common pattern. Two of the most frequently utilized methods are multiple-group principal component analysis (Pimentel, 1979; Thorpe, 1983) and "shearing" (Humphries et al., 1981; Bookstein et al., 1985; Rohlf and Bookstein, 1987). The use of the pooled within-group covariance matrix was criticized by Airoldi and Flury (1988) because it implies the assumption that all within-group covariance matrices are identical. Common principal component analysis has been proposed by Airoldi and Flury (1988) as a statistical model to characterize a common growth pattern under less stringent assumptions.

With real data, however, comparisons of several taxa can also reveal significant differences in growth patterns, as well as general similarities. Therefore, the methods for "size correction" may not always be appropriate. Here we illustrate this point for fish larvae, but we consider it to be of importance for comparative studies of growing organisms in general.

Profiles of allometric coefficients in larvae of several fish species studied by Fuiman (1983) display the same general pattern, but there is also some variation between different species and growth stan-

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TABLE 1. Species considered in this study, sample sizes, and ranges of standard length (in millimeters). Species marked with (G) belong to the order Anacanthini (Gadiformes), and species marked with (P) to the Heterosomata (Pleuronectiformes).

No.	Species[a]	Sample size	Range of STANDARD
1	*Clupea harengus*	50	6.8–19.4
2	*Argentina sphyraena*	48	4.9–18.5
3	*Benthosema glaciale*	52	4.0–8.1
4	*Merluccius merluccius* (G)	45	3.1–7.2
5	*Gadiculus argenteus* (G)	52	2.5–7.3
6	*Merlangius merlangus* (G)	52	2.3–8.0
7	*Micromesistius poutassou* (G)	30	3.5–9.6
8	*Pollachius pollachius* (G)	51	3.1–11.7
9	*Trisopterus* sp. (G)	51	4.5–11.9
10	*Molva molva* (G)	38	3.2–6.7
11	*Scomber scombrus*	45	2.9–9.2
12	*Callionymus* sp.	69	1.9–4.2
13	Triglidae, indet.	37	4.2–15.2
14	*Lepidorhombus boscii* (P)	41	3.5–8.0
15	*Lepidorhombus whiffiagonis* (P)	43	3.5–12.7
16	*Glyptocephalus cynoglossus* (P)	28	3.3–12.5
17	*Microchirus variegatus* (P)	31	2.3–7.0

[a] Names and classification according to Hureau and Monod (1973).

zas. Bivariate plots and multivariate allometric coefficients given by Strauss and Fuiman (1985) show some striking discrepancies in growth patterns between species of one family (Cottidae). Given the extreme changes in both size and shape undergone by many fish species during early ontogeny, and the diversity of body forms they thus achieve, it seems unlikely that there should be a common growth pattern, even within groups of closely related species. Many fish species exhibit simple allometric growth during the postlarval period from the absorption of the yolk sac to the onset of metamorphosis, and thus can be characterized by their allometric growth patterns. This approach is not appropriate, however, if there are several distinct growth stanzas, and it is essential to examine the growth trajectory of each species before analysis.

Patterns of allometric growth in several traits often have been compared by graphic methods (e.g., Fuiman, 1983). Alternatively, allometric patterns, as they are revealed by the vectors of first principal component coefficients (Jolicoeur, 1963), can be treated as multivariate observations characterizing the species from which they were derived. The distribution of the patterns of allometric growth can then be visualized in the space spanned by the allometric coefficients of the original traits. A number of questions arise in this context, some of which we will consider briefly. Are allometric patterns continuously distributed in this coefficient space, or are there discrete "clusters" of patterns displayed by many species, and "gaps" between them, i.e., theoretical patterns that are not realized at all? Is there a connection between similarity in growth patterns and taxonomic relatedness of the respective species? What are the functional and ecological implications of allometric patterns?

In this paper, we characterize 17 taxa of marine fishes by the multivariate allometric patterns (i.e., the vectors of first principal component coefficients) of their larvae. The variation in growth patterns is then summarized in fewer dimensions by principal component analysis, and a small number of "typical" patterns is characterized by principal points (Flury, 1990).

MATERIALS AND METHODS

Most of the fish larvae used in the present study (Table 1) were collected in the Celtic Sea in April 1986 during a cruise of the research vessel *Poseidon* (for details of methods and location, see Röpke [1989]), and a smaller part of the material was ob-

tained from collections of fish larvae at the Institut für Meereskunde, Kiel. All the larvae were stored in buffered 4% formaldehyde solution in fresh water. Although three of the taxa could not be identified to the species level, we will refer to them as species in this paper. Because the samples of these three taxa were fairly uniform morphometrically, each of them probably does represent a single species. The only taxon with two distinct growth stanzas was *Callionymus* sp., where a clear change of the growth pattern occurs at a standard length of about 4.5 mm, coinciding with the differentiation of the preopercular spines (Russell, 1976); the specimens of the second stanza were excluded from analysis, reducing the sample size for this taxon from 84 to 69. As far as possible, we will refer to the species by their generic names, without implying, however, that our results extend to species other than those considered here.

Ten variables were measured in each larva: standard length (STANDARD; length from the tip of the snout to the end of the urostyle), prepectoral length (PREPEC; length from the tip of the snout to the bases of the pectoral fins), body width at the pectorals (PECWID; width of the body above the bases of the pectoral fins), body width at anus (ANALWID; width of the body above the anus), preanal length (PREANAL; length from the tip of the snout to the anus), preorbital length (PREORB; length from the tip of the snout to the anterior margin of the eyes), diameter of the eye (DIAMEYE; measured in dorsoventral direction), depth of the head (HEADDEP; measured at the center of the eyes), body depth at the pectorals (DEPTHPEC; depth of the body at the bases of the pectoral fins, without dorsal fin margin), and depth of the body immediately behind the anus (DEPTHANU; depth of the body without marginal fins). All measurements were taken by the same person (R.F.) using a video system (for further details, see Froese [1990]).

The data were transformed to natural logarithms before analysis. To estimate patterns of multivariate growth allometry, principal component analyses were carried out separately for each species using covariance matrices (Jolicoeur, 1963). Angles between principal components (PCs) were computed as the arccosine of the inner product of the respective PCs (Pimentel, 1979). The bootstrap method (Efron and Tibshirani, 1986) was applied to determine standard errors for the coefficients of the first PCs and the percentages of total variance explained by the first PCs, with 1,000 bootstrap iterations for each species.

To display the variation among multivariate allometric patterns in fewer dimensions, a principal component analysis was performed on the covariance matrix of the allometric patterns, i.e., using the vectors of first PC coefficients of the 17 species as "observations." The resulting principal components are orthogonal axes of maximal variation in allometric patterns among species. However, these components cannot be interpreted in the usual way, and they will only be used to display the variation graphically. Confidence ellipses for the allometric patterns of all species were calculated using the bootstrap estimates from the previous step (for a discussion on the use of confidence ellipses, see Owen and Chmielewski [1985]).

To reduce the number of allometric patterns to be compared, we used a novel approach, principal points (Flury, 1990). Principal points summarize the variation of allometric patterns in a small number of "typical" patterns drawn from the theoretical distribution of allometric patterns in fish larvae, i.e., hypothetical observations that together should be representative of the underlying distribution. The k principal points of a p-variate random vector $\mathbf{X}$ are defined as those points that minimize the expected Euclidean distance of $\mathbf{X}$ from the nearest principal point (Flury, 1990). If $k = 1$, the only principal point is the mean vector of $\mathbf{X}$, and, if $k = N$ in a sample of N observations, each observation is a principal point. Flury (in press) defined the sample mean squared deviation (SMSD), the average squared Euclidean distance between each observation of the sample and the nearest principal point, as

a measure of performance for principal points. If $k = 1$, the SMSD will equal the total variance in the sample (multiplied by $(N - 1)/N$, because $N - 1$ is used as the denominator in the computation of variances), and if $k = N$, the SMSD will be zero because every observation is also a principal point. Between these two extremes, the SMSD falls steeply at the beginning and more slowly as k increases (see examples in Flury [1990, in press]).

When no assumptions about the probability distribution of the observations in a sample are made, the k-means clustering algorithm (e.g., Hartigan and Wong, 1979) can be used to estimate the principal points for a given k (Flury, in press). This algorithm finds k subsets of observations that minimize the sum of squared distances of the points from the nearest group centroid. Thereby, the cluster centroids are estimates of the principal points. The algorithm requires initial guesses on the group centroids (seeds), which are generally chosen from the sample of observations. Depending on the choice of the set of seeds, the algorithm will converge on a local minimum of the within-group sum of squares, which need not be the global minimum of all possible partitions (Hartigan and Wong, 1979; Flury, in press), and therefore the group centroids will not always be valid estimates of the k principal points. We estimated principal points of the 17 allometric patterns for k varying from 1 to 17. The FORTRAN program to estimate principal points used the subroutine KMEAN from the IMSL/STAT program library, which is an implementation of the k-means clustering algorithm of Hartigan and Wong (1979). All possible sets of k points were used as seeds for the k-means clustering algorithm, and the solution with the smallest SMSD was taken as the estimate for the principal points.

Statistical accuracy of principal point estimates was assessed in either of two ways, corresponding to two different sources of statistical error. First, principal point estimates depend on the set of species under consideration; the associated sampling variability was evaluated by a point-deletion procedure, i.e., successively omitting the allometric pattern of each species from the analysis and estimating the principal points using the remaining 16 patterns. Second, the sampling error of the estimates of allometric patterns is another source of error for the principal point estimates of any given set of species; thus, principal points were computed for 100 sets of bootstrap estimates of the allometric patterns of all 17 species. In both kinds of analysis it was not always possible to allocate the principal points of resampled data sets unambiguously to the estimates derived from the original data, and we will therefore only display the results graphically, without giving statistics such as standard errors or confidence intervals.

Results

The first principal components (PCs) explain the largest part of total variance in all 17 species (Table 2). The estimates of the PCs are fairly stable, as can be seen from the relatively small standard errors of the PC coefficients. There is considerable variation among species, as can be seen from the angles between allometric vectors, which range from 3.4° to 23°.

Most PC coefficients clearly differ from 0.316 ($=1/\sqrt{10}$), the theoretical value for isometry (Jolicoeur, 1963). Standard length exhibits negative allometric growth in all species except *Glyptocephalus*, where it is very close to isometry. Negative allometry or isometry is also seen for preanal length. The allometric coefficients of prepectoral length and of the pectoral and anal body widths vary considerably among species. A consistent pattern can be seen in head traits, where the PC coefficients indicate positive allometry for preorbital length and clearly negative allometry for eye diameter in all 17 species. Head depth displays negative allometry, except for *Benthosema* and the two species of *Lepidorhombus*, where it grows isometrically. These three species, *Callionymus*, and *Microchirus* show positive allometry of body depth at the pectorals, whereas *Glyptocephalus* and the Triglidae exhibit isometry and all other species show clearly negative allometric growth in that

TABLE 2. Allometric patterns of fish larvae. First principal component coefficients, percentages of total variance explained, and corresponding standard errors (in parentheses).

Variable	*Clupea*	*Argentina*	*Benthosema*	*Merluccius*	*Gadiculus*	*Merlangius*	*Micro-mesistius*	*Pollachius*
STANDARD	0.262	0.305	0.237	0.241	0.262	0.256	0.261	0.253
	(0.008)	(0.009)	(0.012)	(0.012)	(0.010)	(0.010)	(0.009)	(0.005)
PREPEC	0.280	0.335	0.303	0.301	0.289	0.368	0.350	0.332
	(0.011)	(0.011)	(0.012)	(0.017)	(0.011)	(0.012)	(0.010)	(0.005)
PECWID	0.315	0.264	0.351	0.337	0.357	0.250	0.299	0.309
	(0.026)	(0.020)	(0.017)	(0.024)	(0.013)	(0.021)	(0.011)	(0.008)
ANALWID	0.364	0.323	0.268	0.370	0.378	0.313	0.357	0.364
	(0.025)	(0.019)	(0.021)	(0.019)	(0.017)	(0.018)	(0.015)	(0.009)
PREANAL	0.258	0.317	0.320	0.287	0.259	0.334	0.272	0.239
	(0.008)	(0.016)	(0.012)	(0.011)	(0.006)	(0.008)	(0.007)	(0.016)
PREORB	0.436	0.445	0.329	0.395	0.386	0.397	0.332	0.373
	(0.027)	(0.024)	(0.025)	(0.026)	(0.025)	(0.031)	(0.036)	(0.017)
DIAMEYE	0.237	0.241	0.225	0.219	0.252	0.272	0.295	0.276
	(0.012)	(0.011)	(0.013)	(0.011)	(0.008)	(0.012)	(0.009)	(0.006)
HEADDEP	0.233	0.244	0.312	0.257	0.266	0.262	0.297	0.264
	(0.012)	(0.012)	(0.014)	(0.014)	(0.016)	(0.021)	(0.017)	(0.008)
DEPTHPEC	0.283	0.291	0.387	0.295	0.284	0.277	0.264	0.279
	(0.013)	(0.013)	(0.017)	(0.017)	(0.009)	(0.016)	(0.009)	(0.006)
DEPTHANU	0.417	0.346	0.387	0.402	0.383	0.388	0.404	0.422
	(0.031)	(0.026)	(0.013)	(0.019)	(0.014)	(0.023)	(0.012)	(0.008)
% variance	86.9	91.1	88.5	89.6	92.9	90.2	94.9	97.3
	(2.2)	(1.2)	(1.9)	(1.9)	(1.7)	(1.7)	(1.2)	(0.5)

character. The allometric coefficients for tail depth near the anus clearly exceed the isometric value in all species except *Molva molva*.

To display the variation among allometric patterns, the vectors of first PC coefficients were used as observations for another principal component analysis. However, because the number of observations ($N = 17$ species) is small, the PCs are very unstable and will only be used as a projection of the 10-dimensional space onto a 2-dimensional subspace summarizing the maximal proportion of total variance among allometric patterns. The first PC explains 55% of total variance and the second PC 20%. In Figure 1, the PC scores of the allometric patterns of the 17 species are shown together with the 68% confidence ellipses derived from the bootstrap estimates of the patterns (for comparison: the axes of confidence ellipses at the 95% probability level would be about twice as long as those at the 68% level). The two *Lepidorhombus* species (nos. 14, 15) and *Microchirus* (no. 17) are distinct from all other species. A fairly tight cluster is formed by the growth patterns of five gadoid species (nos. 4, 5, 7–9), *Callionymus* (no. 12), and *Clupea* (no. 1). The allometric patterns of the remaining species are more widely spaced, but there are no really distinct "gaps" between these species.

Principal points were estimated for k varying from 1 to 17, to assess the optimal number of principal points. The k-means algorithm converged on more than one set of points for several values of k (for $k = 4$, 3 sets; $k = 5$, 10 sets; $k = 6$, 17 sets; $k = 7$, 19 sets; $k = 8$, 21 sets; $k = 13$, 3 sets; $k = 14$, 2 sets; $k = 16$, 2 sets). The solution with the smallest SMSD was used as the estimate of the principal points in these instances. Figure 2 shows that the decrease of the resulting values of the SMSD is very steep initially, but rapidly decelerates with increasing k. The curve is fairly smooth, making it difficult to find a cut-off point using objective criteria. However, there is a substantial reduction in the SMSD between $k = 2$ and $k = 3$, and there is no important

TABLE 2. Extended.

Trisopterus	*Molva*	*Scomber*	*Callionymus*	Triglidae	*Lepidorh. boscii*	*Lepidorh. whiffiagonis*	*Glypto-cephalus*	*Microchirus*
0.281	0.227	0.286	0.222	0.247	0.225	0.282	0.317	0.270
(0.012)	(0.015)	(0.009)	(0.008)	(0.010)	(0.017)	(0.007)	(0.019)	(0.010)
0.321	0.314	0.352	0.302	0.283	0.288	0.381	0.379	0.329
(0.013)	(0.028)	(0.008)	(0.009)	(0.008)	(0.022)	(0.016)	(0.017)	(0.014)
0.314	0.341	0.208	0.334	0.297	0.189	0.189	0.265	0.236
(0.016)	(0.052)	(0.013)	(0.012)	(0.019)	(0.038)	(0.016)	(0.040)	(0.026)
0.345	0.356	0.227	0.372	0.273	0.209	0.178	0.284	0.199
(0.015)	(0.027)	(0.011)	(0.010)	(0.024)	(0.025)	(0.013)	(0.021)	(0.015)
0.270	0.288	0.324	0.232	0.276	0.250	0.272	0.300	0.300
(0.008)	(0.019)	(0.006)	(0.008)	(0.009)	(0.015)	(0.006)	(0.013)	(0.009)
0.381	0.497	0.490	0.424	0.405	0.330	0.338	0.445	0.346
(0.030)	(0.040)	(0.014)	(0.018)	(0.023)	(0.039)	(0.018)	(0.034)	(0.039)
0.279	0.218	0.273	0.235	0.284	0.186	0.202	0.185	0.150
(0.010)	(0.020)	(0.008)	(0.009)	(0.016)	(0.022)	(0.008)	(0.011)	(0.008)
0.232	0.225	0.221	0.291	0.293	0.314	0.318	0.244	0.290
(0.018)	(0.034)	(0.014)	(0.010)	(0.021)	(0.019)	(0.017)	(0.017)	(0.012)
0.250	0.286	0.278	0.327	0.322	0.439	0.410	0.320	0.415
(0.008)	(0.017)	(0.009)	(0.009)	(0.017)	(0.014)	(0.012)	(0.025)	(0.015)
0.435	0.312	0.393	0.360	0.431	0.539	0.458	0.350	0.485
(0.011)	(0.030)	(0.011)	(0.010)	(0.015)	(0.017)	(0.012)	(0.027)	(0.027)
92.0	78.2	95.2	92.6	93.5	86.0	95.1	86.4	91.2
(1.3)	(4.4)	(1.1)	(1.0)	(1.8)	(4.0)	(0.7)	(3.9)	(1.3)

further reduction for $k > 5$. We feel that $k = 4$ is the most reasonable choice.

The estimated principal points for $k = 4$ are plotted in Figure 3a (triangles), and the corresponding allometric patterns are given in Table 3. Point no. 1 corresponds to three of the flatfishes, i.e., the two *Lepidorhombus* species and *Microchirus*. The allometric pattern of this point is characterized by markedly negative allometry of the pectoral and anal widths and of the eye diameter, whereas the body depths at the base of the pectorals and at the anus exhibit strongly positive allometry. The Triglidae and *Benthosema* are allocated to point no. 2. The corresponding growth pattern shows positive allometry in depth measurements similar to the pattern of point no. 1, from which it is distinguished, however, by nearly isometric growth of the body width traits and the less extreme negative allometry of the eye diameter. The estimated principal point no. 3 is associated with *Scomber, Glyptocephalus, Argentina,* and *Merlangius*. This point differs from the others by the stronger relative growth of length measures, standard length displaying only slightly negative allometry, preanal length being very close to isometry, and the preorbital and prepectoral lengths being more positively allometric than in any of the other points, whereas depth and width measurements show negative allometry or (for DEPTHANU) lower coefficients than the other points. *Clupea, Callionymus,* and all the gadoid species (except for *Merlangius*) are allocated to point no. 4. The growth pattern corresponding to this point is characterized by markedly positive allometry of the anal body width and, to a lesser extent, of the pectoral body width.

The results of the point-deletion analysis (Fig. 3a) show that three of the principal point estimates are relatively stable, i.e., there are only small changes in their positions if one species is excluded from the analysis. Many of these points coincide with the estimated principal points of all 17 growth patterns. Point no. 2, however,

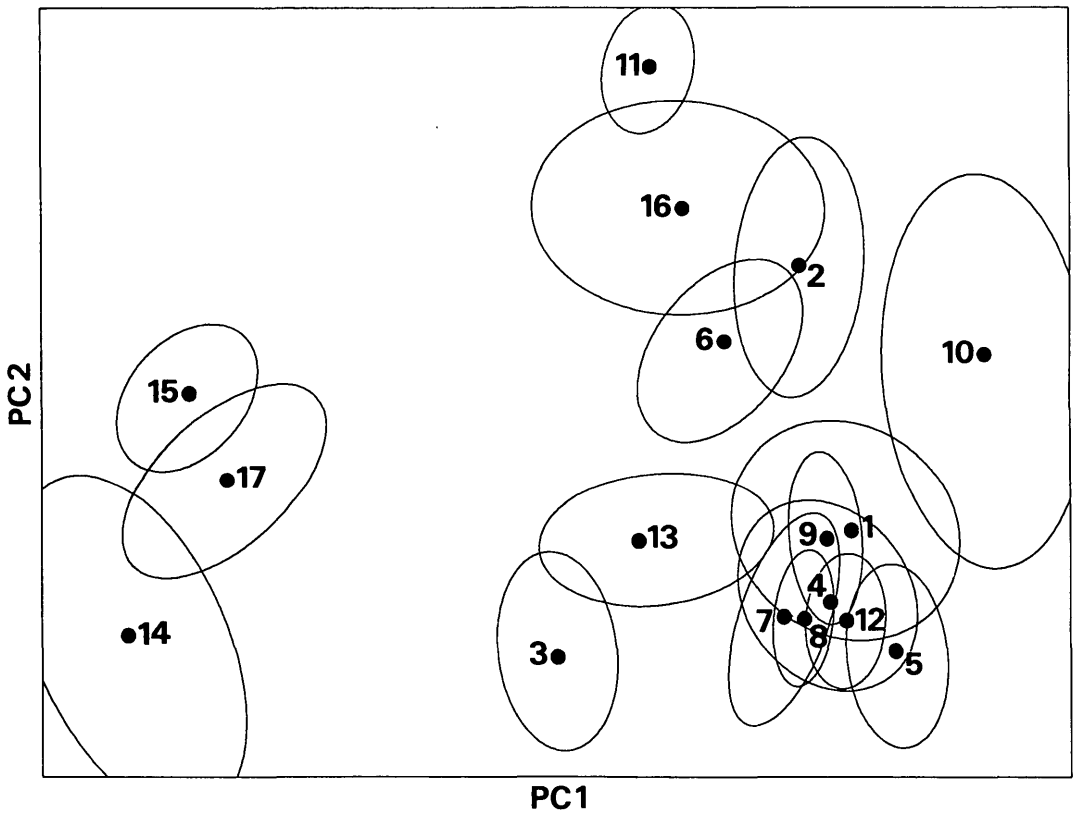

FIGURE 1. Principal component analysis of multivariate allometric patterns in larvae of 17 fish species. PC scores of the allometric patterns of each species and 68% confidence ellipses derived from the respective bootstrap estimates are plotted. The species are numbered as in Table 1.

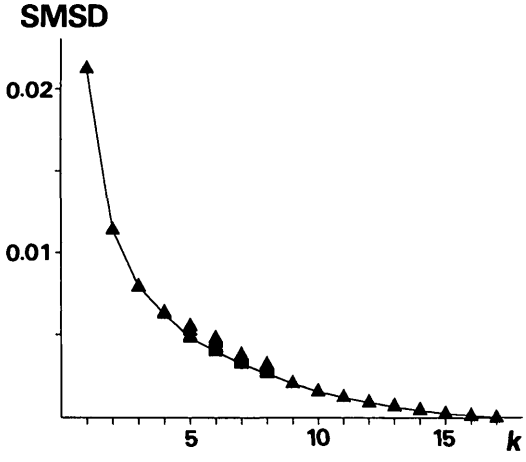

FIGURE 2. Sample mean squared deviations (SMSD) for k ranging from 1 to 17. Triangles give the SMSD values for all sets of points where the k-means algorithm converged. The line joins the lowest SMSD values (corresponding to the principal points) for every k. See text for further explanation.

shifts far toward point no. 4 when *Benthosema* is omitted (Fig. 3a, arrow), and *Molva* may be allocated to either point no. 3 or no. 4, depending on the species excluded.

The principal points estimated from sets of bootstrap estimates of allometric patterns (Fig. 3b) form distinct "clouds" surrounding the original principal point nos. 1, 3, and 4, indicating that these points are fairly well defined. The "cloud" around point no. 2, however, is not as well delimited as those of the other principal points, and is somewhat difficult to separate from the "cloud" of point no. 4. A few of the principal point estimates are interspersed, without clear relation to one of the four main clouds, corresponding to combinations of extreme bootstrap estimates of the allometric patterns.

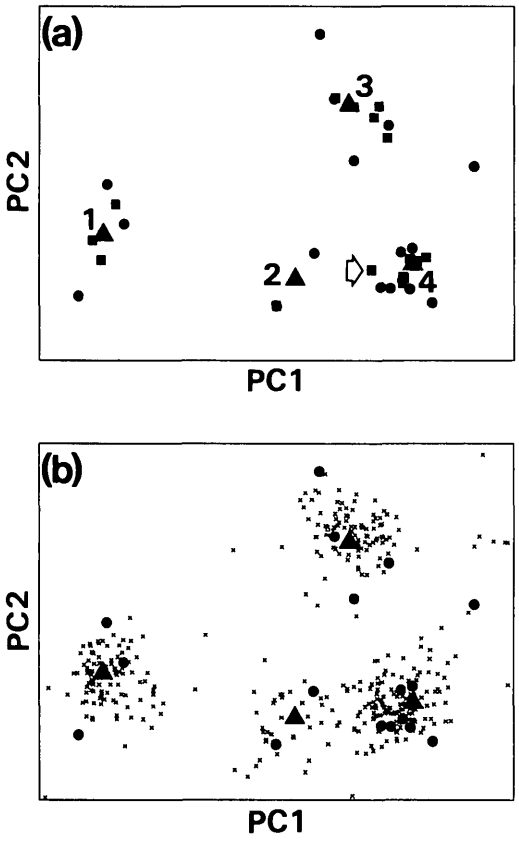

FIGURE 3. Plots of the principal component scores of allometric patterns (dots; as in Fig. 1) and the estimated principal points (triangles) for $k = 4$. (a) Point-deletion analysis for principal points. Squares represent principal points computed with one allometric pattern excluded from the analysis. The arrow indicates the position of principal point no. 2 when *Benthosema* is omitted. Principal points are numbered as in the text and in Table 3. (b) Principal points (marked with ×) for 100 sets of bootstrap estimates of allometric patterns of the 17 species.

TABLE 3. Allometric patterns of estimated principal points for $k = 4$.

Variable	Principal point no. 1	2	3	4
STANDARD	0.259	0.242	0.291	0.251
PREPEC	0.333	0.293	0.358	0.311
PECWID	0.204	0.324	0.247	0.326
ANALWID	0.195	0.271	0.287	0.363
PREANAL	0.274	0.298	0.319	0.263
PREORB	0.338	0.367	0.444	0.403
DIAMEYE	0.179	0.254	0.243	0.251
HEADDEP	0.307	0.302	0.243	0.258
DEPTHPEC	0.421	0.354	0.291	0.284
DEPTHANU	0.494	0.409	0.369	0.392

DISCUSSION

Principal component analyses revealed a considerable amount of variation among patterns of allometric growth in larvae of 17 fish species. There is a broad overlap in the bootstrap estimates of some allometric patterns, but there are also clear "gaps" (see Fig. 1). The hypothesis of an allometric pattern common to all 17 species must therefore be rejected. However, the number of species in the present study is insufficient for generalizations on the distribution of growth patterns in fish larvae, and it is impossible to decide whether the gaps between different patterns are due to the existence of distinct types of multivariate growth, or whether they result from poor sampling of growth patterns continuously distributed in the space of allometric coefficients.

Taxonomic relations between the species are not directly reflected by the similarity of the respective allometric patterns. The fairly dense cluster formed by five of the seven species from the order Anacanthini also contains *Clupea* and *Callionymus*, which are not closely related to that order. On the other hand, two of the six species of Gadidae (*Molva* and *Merlangius*) have growth patterns distinct from the other four. Three flatfish species (the two *Lepidorhombus* species and *Microchirus*) form a group that is clearly separated from all other species, including the fourth flatfish considered here (*Glyptocephalus*). This reflects the diversity of larval forms within the order Heterosomata: the Scophthalmidae (including *Lepidorhombus*) and Soleidae (including *Microchirus*) having deep-bodied larvae, and the Pleuronectidae (including *Glyptocephalus*) having elongate larvae (Ahlstrom et al., 1984). The angle between the allometric vectors of the two *Lepidorhombus* species is 8.3°. The difference in the allometric patterns between these two congeneric species is considerable, compared to the variation of patterns of different genera

within the Gadidae. Therefore, even closely related species need not be very similar in their patterns of allometric growth. However, other studies found a closer correspondence: e.g., Boitard et al. (1982) in a complex of four isopod species and their hybrids, and Klingenberg and Zimmermann (in press) in nine species of two genera of waterstriders.

Because allometric patterns can differ significantly even between closely related species, techniques for "size correction," which all require a pattern of growth common to the groups under consideration (Rohlf and Bookstein, 1987; Airoldi and Flury, 1988), should not be applied without prior examination of the variation within groups. The underlying model that the taxa under consideration share a common growth pattern should be tested explicitly whenever possible. A specific test is available for common principal component analysis (Flury, 1988). The bootstrap technique may be helpful when parametric tests are not applicable because their assumptions (e.g., multivariate normal distribution) are not fulfilled. The hypothetical common pattern is then compared with the bootstrap estimates of the allometric pattern for each species. The "gaps" between patterns in Figure 1 show that no growth pattern is common to all 17 species in the present data set.

If one is interested exclusively in the separation of the species under consideration, errors caused by violating the assumption of equal allometric patterns need not altogether invalidate the results of the analysis. However, it must be kept in mind that "size correction" in these cases will not yield patterns of variation among groups independent of the variation within groups ("size"). A simple graphic method to avoid these problems is the "tomographic presentation" of Boitard et al. (1982), which uses a principal component analysis of the pooled samples. The scores of the second and subsequent principal components are plotted separately for several levels of first principal component scores. Because the first principal component of the pooled samples is often highly correlated with first within-group principal components, this method allows comparison of the variation among groups at different levels of "size" without making any assumptions about the patterns of allometric growth of the groups under consideration.

To facilitate comparison of growth patterns in the absence of an allometric pattern common to all the species under consideration, one can look for a small number, k, of "typical" patterns that optimally characterize the observed distribution. Principal points (Flury, 1990) give such patterns for any distribution with finite variances. In our example, we can reduce the points to be compared to four principal points instead of the allometric patterns of all 17 species. All four estimated principal points of our data set have several features in common. The eye diameter exhibits clearly negative allometry. Standard length and preanal length show negative allometry or isometry, whereas body depth behind the anus exhibits strongly positive allometry. Therefore, the body, and especially its posterior part, becomes relatively shorter and stouter with increasing size of the larva. This is probably related to the change in swimming style during larval growth, associated with increasing importance of the tail region for locomotion (e.g., Webb and Weihs, 1986). Preorbital length shows positive allometry for all four points, reflecting the elongation of the anterior part of the head, which results in enlargement of the mouth, allowing the larvae to feed on larger food items.

The width and depth measures contribute most of the variation between estimated principal points. Point no. 1 is characterized by negative allometry of body widths and positive allometry of body depths, corresponding to the lateral compression typical of the adult body form of these three flatfishes. On the other hand, species with very diverse larval and adult body forms are allocated to the other principal points, especially to point no. 3. Therefore, variation in allometric growth patterns among species is only partly consistent with variation in body forms of lar-

vae (Froese, 1990) or adults, and various combinations of initial body forms and growth patterns can achieve a diversity of juvenile and adult forms. Strauss and Fuiman (1985) found that the interspecific morphometric differences in larvae closely correspond to those in adults of five species of Cottidae. This result is not confirmed in the present study for a more diverse spectrum of species.

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