Quantitative comparisons of body form and allometry in larval and adult Pacific sculpins (Teleostei: Cottidae)

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Morphometric analyses of body form were performed on samples of larvae and adults of five Pacific sculpin species (Ascalophus rhodorus, Clinocottus acuticeps, Enophrys bison, Nautichthys oculofasciatus, and Rhampocottus richardsoni) to investigate patterns of interspecific variation, intraspecific differences in allometry between larvae and adults, and relative shape changes that occur in the transformation from larva to adult. Within species, larvae are relatively more variable at a given size than adults, while adults are more variable among species because of divergence during development. Much nonallometric change in shape occurs during transformation, but the relative amount of change varies among species. The direction of change during transformation is not predictable from larval morphology alone. Some pairs of species become convergently similar during transformation, some change in parallel, and others become highly divergent in form.


Des analyses morphométriques de la forme chez des larves et des adultes de cinq espèces de Cottidae du Pacifique (Ascalophus rhodorus, Clinocottus acuticeps, Enophrys bison, Nautichthys oculofasciatus et Rhampocottus richardsoni) ont permis de déterminer la variation interspécifique, les différences intraspécifiques d’allométrie chez les larves et les adultes et les changements relatifs de la forme au cours de la transformation de la larve en adulte. Chez une même espèce, les larves sont relativement plus variables que les adultes à une taille donnée; la variation entre les adultes est surtout intraspécifique, à cause de la divergence au cours du développement. Il se produit des changements non allométriques de la forme au cours de la transformation, mais l’importance relative des changements varie d’une espèce à l’autre. La direction des changements au cours de la transformation n’est pas prévisible seulement à partir de la morphologie de la larve. Quelques paires d’espèces subissent une certaine convergence au cours de la transformation, certaines subissent des changements parallèles et d’autres acquièrent une forte divergence de forme.

The study of morphological variation among species for ecological or evolutionary purposes has conventionally been based on comparisons of adult forms. Only recently have quantitative comparative studies of early life-history stages been undertaken. A substantial amount of the morphological variation expressed by larvae is due to allometry, the systematic change in shape with growth. The ultimate goal of morphometric studies is to quantify shape differences, allometric or nonallometric, within the context of a particular set of questions or hypotheses. There have been countless morphometric studies of adult fishes, but only a few authors have examined shape change in fish larvae. These include single-species accounts (Doan 1939;Gihr 1957; Yeager and Wallus 1982) and multiple-species comparisons of larvae (Fuiman 1979, 1983).

Martin’s (1949) experimental study on effects of temperature and diet on body form included larger larvae, juveniles, and adults. All of these studies were based on bivariate analyses of linear measurements, mostly along the longitudinal body axis, yielding information about allometry in only one direction. Strauss and Bookstein (1982) discussed the inadequacies of such morphometric techniques and described the two-dimensional geometric methods of shape analysis that we use here.

Conceptually, it is self-evident that interspecific differences in relative size and shape of homologous structures in adults result from differences in ontogeny. However, it is also reasonable that many observed morphological similarities among adults, especially of species occupying similar habitats, might arise from different but convergent patterns of development. To what degree does similarity in adult morphology reflect similarity in larval morphology and underlying patterns of development? An attempt to answer this question must involve simultaneous comparisons of larval and adult body forms on a common operational basis. This raises methodological problems. How may we describe body form in larvae and adults in such a way that they can be meaningfully compared? Such comparisons would allow us, among other things, to (i) contrast inherent variability in larvae with that in adults; (ii) quantify the amount of transformation (change in form) from the larval phase to the adult; (iii) quantify the relative amounts of divergence or convergence in adult body form with respect to larvae (that is, describe and compare ontogenetic trajectories of form among sets of species); (iv) assess the degree to which differences in form among larvae of different species constrain or “predict” observed differences among adults; and (v) determine whether observed forms of adults allow “predictions” of body forms of larvae not yet described.

We present here an exploratory analysis of patterns of growth and development of body form for five species of Pacific sculpins. We suggest methods for comparing general

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aspects of body form of larval and adult fishes, and show how the application of these methods yields some insight into patterns of convergence and divergence during growth of these five species.

Methods

We examined five species of Pacific sculpins for which both larvae and adults of sufficient size range were available: Ascleliothys rhodorus (16 larvae, 4.1–13.5 mm standard length (SL); 14 adults, 46.8–81.2 mm SL); Clinocottus acuticeps (22, 7.3–12.7 mm; 26, 30.6–42.1 mm); Enophrys bison (24, 5.2–9.2 mm; 30, 49.9–111.0 mm); Nautichthys oculofasciatus (20, 8.2–13.2 mm; 18, 75.6–110.4 mm); and Rhamphocottus richardsoni (9, 7.4–9.9 mm; 16, 25.4–53.1 mm). Larvae had been reared from eggs in the laboratory and preserved in formalin, as described by Matarese and Marliave (1982). All specimens had been stored in formalin for at least 1 year before examination. Standard length in larvae was measured from the tip of the snout to the end of the urostyle (before notochordal flexion) or to a point at the base of, and between, the central caudal-fin rays. Because each species represents a different genus, we refer to them by their generic designations but do not mean our results or conclusions necessarily to apply to other members of these genera.

Measurements

Our goal was to measure differences in lateral body outlines in terms of localized anatomical landmarks hypothesized to be homologous among species. To do this we assigned two sets of midsgatittal landmarks, one set for larvae and one for adults (Fig. 1). Larvae had few landmarks in common with adults and so the two sets were characterized independently. Landmarks on larvae were the medial tip of the snout (landmark 1); the ventral intersection of the cleithrum with the midsgatittal outline (2); the tip of the urostyle (before flexion) or the base of central caudal-fin rays (postflexion) (5); the dorsal intersection of the 1st myoseptum (8); and the dorsal and ventral intersections of the 1st postanal (7, 3) and 27th myoseptum (6, 4) with the midsgatittal outline. The first postanal myoseptum was defined as the first myoseptum to meet the ventral fin fold behind the anus. The 27th myoseptum was chosen as a source for landmarks to describe the shape of the posterior portion of the body because all five species possessed at least 27 myomeres. Landmarks for adult sculpins were the medial tip of the premaxilla (landmark 1); the anterior margin of the frontal bones (located by local dissection) (10); the insertions of the anterior spines or rays of the dorsal (8, 9), pelvic (2), and anal (3) fins, and the posterior rays of the second dorsal (7) and anal (4) fins; and the insertions of the dorsal (6) and ventral (5) procurent caudal-fin rays.

Relative positions of landmarks for larval specimens were transferred to paper with a camera-lucida attached to a Wild M5 dissecting microscope. Polarized transmitted light was used to locate landmarks accurately. Landmarks for adults were transferred to paper by means of a pantograph. For both larvae and adults, landmark configurations on paper were digitized electromagnetically (Houston Instrument Hipad digitizing tablet) into a computer file as relative Cartesian coordinates.

Lengths between landmarks were computed as Euclidean distances adjusted for differences in scale. Distance measurements were selected to form “trusses” (Strauss and Bookstein 1982), geometric arrangements that are highly sensitive to changes in size and shape among forms and that yield adequate descriptions of shape in the absence of prior knowledge about variation in form. These configurations allowed us to reconstruct original forms from sets of distances among landmarks, and to average the forms of a sample to compute and illustrate average shapes standardized to a common measure of body size. Adult forms were represented by four truss cells describing the head, midbody, trunk, and tail (peduncle) regions (Fig. 1). Larvae were represented by two central truss cells describing midbody and trunk, and two terminal triangles representing the head and tail. Methods of manipulating truss configurations for quantitative comparisons were described by Strauss and Bookstein (1982).

To facilitate comparisons between larvae and adults despite the independence of the two data sets, composite length and depth dimensions were estimated for each of the four body regions described by either a truss cell or a triangle. For each truss cell, mean length was estimated as the average of the dorsal and ventral “horizontal” elements, while mean depth was the average of the anterior and posterior “vertical” distances. For the terminal triangles of larval forms, mean depth was taken to be half the length of the single vertical element (the distance measurement shared with the adjacent truss cell) and mean length was the average of the two remaining elements. We refer to these eight average dimensions as regional characters.

Statistical comparisons

We explored patterns of variation using principal component analysis, a widely used, sensitive multivariate technique which summarizes the primary trends of variation within a data set, reducing these trends to a small number of independent variables that incorporate the original information. Principal components (PCs) were computed from the covariance matrix of logarithmically transformed distance measurements. The logarithmic transformation produces a covariance matrix independent of scaling, but preserves allometries (Jolicoeur 1963). Our samples of each species contained individuals that varied significantly in body size; consequently the first within-group component (PC1) was a measure of “general size,” summarizing the joint size increase in all distance measurements and providing a standard measure with which growth in individual measurements was compared. Because we used only midsgatittal landmarks, general size was highly correlated with the area of the midsgatittal projection. The loadings of individual distance measurements on the within-group PC1 were rescaled (so that their squares summed to the number of measurements) and interpreted as multivariate allometric coefficients on general size (Chernoff and Miller 1982; Leamy and Bradley 1982; Strauss and Bookstein 1982). These coefficients indicate the manner in which different distance measurements change in relation to overall body size. Values greater than unity describe positive allometry, those less than unity indicate negative allometry. In analyses of two or more species, PC1 likewise accounts primarily for variation in size, although the loadings in this case reflect average size-related changes among the species. In all of our among-group analyses a substantial amount (>97%) of residual
variation was accounted for by PC2 and PC3, which described contrasts in shape among samples. The loadings on these components indicate the degrees to which individual morphometric measurements contribute to shape differences. Minor correlations of these secondary components with body size were removed by “shearing” the components (that is, regressing out the pooled within-group PC1) to ensure that they represented shape differences independent of body-size variation (Humphries et al. 1981).

After principal components were computed, a set of scores was calculated for each individual, representing its projection onto the component axes. These scores were used to produce scatters of individuals in the plane formed by two components. We computed the correlations of scores with the composite regional characters to graphically interpret observed variation on principal components in terms of regional body form.

Results

Allometric comparisons

The first within-group principal component is a highly consistent measure of general size in these species, despite their rather large differences in form. For both larvae and adults, within-group size vectors (PC1) have positive loadings for all characters and account for 90—97% of total variance. Vector-correlation coefficients, which measure the similarity of size vectors for pair-wise comparisons of samples (Bryant 1984), range from 0.99 to 1.00 for larvae and from 0.98 to 1.00 for adults. Use of the loadings of the within-group PC1 as multivariate allometric coefficients therefore allows us to assess and compare overall patterns of differential relative growth. Because these allometric coefficients are derived from a sample of individuals each measured once, they may not strictly represent patterns of growth (Cock 1966). However, the patterns of multivariate allometry do account for variation in form within samples and for differences in shape between species.

Patterns of differential growth vary significantly, both within species (between larvae and adults) and among species (Figs. 2 and 3). In larvae there is a general tendency for the head to lengthen more rapidly than the midbody and trunk, a pattern consistent with, though not as well defined as, the U-shaped growth gradients described by Fuiman (1983) for several other teleost larvae. In these sculpins, however, the tail is highly negatively allometric, growing either much more slowly than the head and midbody regions (in Ascelichthys and Clinocottus) or apparently shortening as the fish grows (in Nautichthys, Rhamphocottus, and Enophrys). This is due in part to negative allometry of the region and in part to caudal flexion of the urostyle, with an accompanying shift in landmark 5. All species except Rhamphocottus show a significant relative increase in depth in the midbody and trunk.

There seem to be no consistent directional patterns of relative growth among adults (Fig. 2) except for a tendency for the peduncle to become more slender and elongate. The changes in shape that take place during juvenile and adult growth are instead due to relative changes in fin positions and body profile, leading to extremely different body forms among species.

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Fig. 3. Scatters of depth versus length of each body region for larvae and for adults of five species of sculpins. Solid lines are principal axes of clusters. Broken lines represent hypothetical growth stanzas during transformation. Numbers along solid lines are bivariate allometric coefficients of depth with respect to length. Axes are logarithmic.
Shape comparisons

Differences in larval body form among the five species, apparent in the averaged shapes depicted in Fig. 2, are summarized by a principal component analysis of the 15 morphometric measurements (Fig. 4). The second and third components were sheared to remove residual size effects, although the vector correlations of the sheared components with the corresponding original components were both greater than 0.98, indicating that the size effects removed were very small. Correlations of the eight regional characters (which were not directly included in the principal component analysis) with the components portray the manner in which the first three components account for shape variation among species, and the manner in which the regional characters covary within and among species.

As expected, PC1 accounts primarily for variation in larval size. All aspects of regional shape covary strongly except for trunk length and tail length, both of which tend to be negatively allometric within species (Fig. 4a). Sheared PC2 and sheared PC3 describe shape differences among species. PC2 accounts primarily for the tradeoff between body length and body depth at a given body size: Nautichthys and Ascelichthys larvae are relatively long and slender, while larvae of the other three species are relatively deep-bodied. PC2 also describes systematic interspecific differences in the shape of the separate body regions. PC3 provides a minor contrast between species that possess relatively large tails and short midbody regions (Ascelichthys and Enophrys), and those that are longer in the midbody and have smaller tails (Clinocottus and Nautichthys).

That these multivariate descriptions of shape differences among larvae are meaningful and predictive is shown by the high congruence of this analysis with a parallel analysis of adults based on 21 morphometric measurements (Fig. 5). Although the interspecific differences among adults are much more trenchant than those among larvae, the contrasts in shape that differentiate larvae are similar to those that differentiate adults. In particular, sheared PC2 again describes the basic contrast between relative body depth and body length, especially of the trunk and tail. The sequence of species on PC2, the primary adult shape axis, is the same as on the larva shape axis except that Ascelichthys and Clinocottus are relatively more similar to one another as adults than as larvae.

Larva—adult transformations

To describe the relative transformations in shape from larva to adult, the multivariate shape information expressed by these separate principal component analyses may be summarized in a single diagram (Fig. 6a). Ignoring the minor contrasts described by the third and subsequent components, the scores on sheared PC2 for larvae and for adults were scaled to have equal grand means and ranges. Because these scores are independent of within-group size, the shape changes depicted by the diagram represent only the relative transformations from larva to adult. The scaling we used forces the trajectories for Nau-
tichthys and Rhamphocottus (at the extremes of the axes) to be parallel; the other three trajectories depict shape change relative to these two species. The transformation of Enophrys seems to parallel that of Rhamphocottus and Nautichthys, while those of Aselichthys and Clinocottus converge and cross. The resulting shape changes can be envisioned from the correlations of the regional characters with the shape axes of Fig. 6a (and from the averaged forms of Fig. 2). Any “vertical” displacement along the shape axis describes changes in the dimensions having the largest correlations with the axes, in this case lengths of midbody, trunk, and tail. For example, the convergence of Aselichthys and Clinocottus involves a relative shortening of these three body regions in the former and a lengthening in the latter, with no appreciable change in relative head size. Such transformations in shape indicate the presence of growth stanzas with characteristics of growth and shape change different than those of the larva and adult.

To examine these ontogenetic transformations on a common scale of measurement rather than on two separate scales arbitrarily made equal, a pooled analysis was done using the eight (log-transformed) regional characters for larvae and adults (Fig. 6b). The common scale is the sheared PC2 from the pooled analysis. This pooled analysis sacrifices much of the information contained in the original distance measurements, but permits a better assessment of relative shape and of relative variability of shape. On a common scale, the transformation of Rhamphocottus is highly divergent from the others, even though the larvae of Rhamphocottus and Enophrys are initially similar in form. The transformation of Clinocottus is again shown to be convergent with that of Aselichthys, while the transformations of two species pairs are approximately parallel: Nautichthys and Aselichthys, and Clinocottus and Enophrys. The loadings of the eight characters on sheared PC2 (Fig. 6b) are highly consistent with their correlations on the separate larva and adult shape axes (Fig. 6a), indicating that all three analyses bear the same information about relative length and depth of the four body regions.

In all cases larvae are relatively more variable in morphology than adults. (On a logarithmic scale, equal variances across size imply equal coefficients of variation for the original distance measurements.) Although this may be partly artifactual, because of differences in mensural technique for larvae and adults, preliminary studies of measurement replicability indicate that it is unlikely that the two- to three-fold difference in variability observed is completely artifactual. For larvae and adults separately there is no clear statistical relationship between size and variability (Fig. 3).

Discussion

One important goal of biological morphometry is the quantitative comparison of organisms as ontogenetic trajectories (life cycles) that react to short-term ecological responses and long-term evolutionary development (Bonner 1965, 1982). To attain this we need at the very least an operational basis for treating different life stages within the same mensural scheme, and analytic methods for comparing organisms as ontogenies rather than as representatives of single life-history stages. Such studies of fishes are difficult because of the apparent dearth of
FIG. 6. (a) Relative transformations in shape (mean scores on the sheared second among-group principal component) from larva to adult, based on independent analyses of the two stages using 15 and 21 characters, respectively (Figs. 4 and 5). Shape axes are scaled to equal ranges and means. Vertical arrows to the right indicate relative correlations of the eight regional characters with the shape axis. For each character the left (dotted) arrow is from the larva analysis (Fig. 4b), the right (broken) from the adult analysis (Fig. 5b). (b) Relative transformations in shape based on a pooled analysis (sheared second component) of larvae and adults using the eight regional characters. Vertical arrows indicate relative character loadings.

consistently measurable characteristics that can be observed in both larval and adult stages.

Our study has shown that sets of distance measurements in the form of closed geometric configurations (trusses and triangles among morphological landmarks) describe regional body form in such a way that the morphology of larvae and adults can be meaningfully compared, despite the differences in the particular landmarks used for each life stage. Our quantitative comparisons have indicated that (i) larvae seem to be inherently more variable within species than adults, while adults are more variable among species because of divergence during development; (ii) a considerable amount of change in form takes place during the transformation from larva to adult, but the relative amount of change varies among species; and (iii) in some species pairs (for example, Ascelichthys and Clinocottus) body form converges during the transformation, in others (such as Clinocottus and Enophrys) it changes in parallel, while in still others (such as Enophrys and Rhamphocottus) it diverges greatly.

At least in these five species, the differences in body form that distinguish among larvae are the same as those that distinguish among adults. In this sense the larval form does “predict” and constrain the resulting adult form, in spite of a considerable amount of convergence and divergence among species during growth. This suggests that multivariate analyses of adult forms may provide an indication of the morphometric measurements most likely to discriminate among larvae of the same species. The congruence we observed, however, is probably due in part to the very large morphological differences among the five genera studied. Consequently, interesting questions for future investigations would be whether or not differences in body form among larvae are the same as those among adults for more closely related (intragenic) pairs of species, and if so, to what extent we can predict the morphology of undescribed larval forms from the morphology of the adult, given knowledge about the ontogenetic development (morphology of larva and adult) of its close relatives. This will depend on the degree to which developmental trajectories like those of Fig. 6 are parallel.

There have been few attempts to compare ontogenetic sequences of development in fishes, especially among species that exhibit distinctive larval forms. However, it is clear that diversification of many groups of fishes and other organisms has been correlated with shifts in ontogenetic development that have resulted in major morphological and ecological changes (Liem 1973; Alberch 1980; Strauss 1984). Alberch et al. (1979) and Creigton and Strauss (1985) have attempted to provide models in which ontogenetic sequences can be quantified and compared as ontogenetic trajectories.

This study was intended to be exploratory, and could be extended in two primary directions. First, because of the morphological sensitivity of fish larvae to environmental influences (Martin 1949; Valentine and Soulé 1973; Lindsey and Arms 1981), an examination of patterns of morphological development may greatly increase our ability to detect chronic ecological perturbations. We hypothesize that such physiological disturbances would affect both the direction and amount of morphological transformation from larva to adult by altering relative growth rates and timing. Second, there has been much recent interest in the utility of ontogenetic studies for construction of phylogenetic hypotheses (Moser and Ahlstrom 1974; Fink 1982; Moser et al. 1984). With a suitable choice of taxa, including appropriate out-groups, quantitative ontogenetic studies such as those of Fuiman (1984) and Creigton and Strauss (1985) may add a dynamic component to the assessment of morphological similarity, thus providing a more robust procedure for detecting evolutionary parallelism and convergence than conventional static comparisons of adult form.

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