Visualizing Allometry: Geometric Morphometrics in the Study of Shape Changes in the Early Stages of the Two-Banded Sea Bream, Diplodus vulgaris (Perciformes, Sparidae)

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ABSTRACT The sea bream, Diplodus vulgaris, is a marine teleost widely distributed in the Mediterranean and eastern Atlantic coastal waters. The larvae colonize shallow waters along rocky shores where, after a short period spent in the water column, they settle. Such habitat transition is characterized by important shape changes, mostly related to their swimming capacity and feeding behavior. In this study, geometric morphometrics has been used to characterize shape changes during early juvenile life. All specimens were collected in a single locality in the Gulf of Tigullio (Ligurian Sea), and data relative to their position in the water column and to the habitat selected were recorded. A total of 14 landmarks were collected on 82 specimens (range of standard length 11.2–82.8 mm). Landmark configurations were superimposed, and residuals were modeled with the thin-plate spline interpolating function: shape changes were visualized as splines. Growth trajectories were computed using relative warp analysis. Shape changes in the observed size range concern an overall broadening along the dorsoventral axis, a displacement of the mouth position, and a negative allometry of the head region. The growth trajectory resembles a theoretical saturating growth curve: shape change is fast for small sizes and slows down at standard lengths of approximately 28 mm, where an increase in size is not accompanied by a change in shape. This size value corresponds roughly to the size at which the settlement and the successive phase of dispersion of D. vulgaris have been observed in the area of study. This approach provides quantitative descriptors of shape changes and allows for the visualization of allometry. This method implies the definition of a new space for biological shapes in which shape trends and clusters can also be identified in relation to nonmorphological variables. As such it might contribute to the definition of the morphospace in the context of ecomorphology. J. Morphol. 237:137–146, 1998.

KEY WORDS: Diplodus vulgaris; allometry; geometric; morphometrics

The sea bream, Diplodus vulgaris (Pisces: Perciformes, Sparidae) is a marine teleost widely distributed on the Mediterranean and eastern Atlantic coasts. Like other marine littoral fish species, it has a life cycle that consists of a pelagic dispersal larval phase followed by a sedentary benthic adult phase (Richards and Lindeman, ’87; Jug-Dujakovic and Glamuzina, ’88). At the end of the planktonic stage, surviving larvae colonize shallow waters (up to 2 m deep), along rocky shores where, after a short period spent in the water column (0–0.5 m deep), they settle on boulder substrates (Harmelin-Vivien et al., ’95). The transition from pelagic to benthic life is considered a critical period of the life cycle of D. vulgaris in which perturbances might severely influence the recruitment of the species. Such transition involves several changes mainly concerning denti-
tion, feeding behavior, and swimming capacity (Brothers and McFarland, '81; Stoner and Livingstone, '84). These changes are accompanied by the acquisition of a new body shape. Starting from streamlined profiles suitable for periodic thrusts in the water column (Webb, '84) typical of pelagic juveniles, the late juveniles of D. vulgaris are characterized by broad profiles that are better suited for maneuvering. In addition to this new shape, size determines the relationship between the small fish and its medium: viscous or inertial regimes characterize different size ranges (Muller and Videler, '96), strengthening the relationship between size, shape, and performance. In this study, geometric morphometrics (Bookstein, '91; Rohlf and Marcus, '93; Marcus et al., '96) has been used to characterize growth trajectories (Alberch et al., '79) and to visualize these size-related shape changes, i.e., growth allometry (Klingenberg, '96), during this period of transition. The relation between shape changes, a specimen's position in the water column, and the habitat selected is described.

MATERIALS AND METHODS

Sampling and visual inspection

All specimens (82 individuals) of D. vulgaris were collected in one single locality near Portofino's promontory (Ligurian Sea; Fig. 1). Data relative to their position in the water column and to the habitat selected were collected by visual inspection. Sampling was carried out during the spring and summer of 1994, 1995, and 1996, using a beach seine. All samples were preserved in 40% alcohol. During this 3-year survey (33 records), habitat choice and depth of the observation were recorded for a total of 885 specimens.

Geometric morphometrics

The population of the two-banded sea bream considered was studied by the application of allometric models to the distribution of forms in the tangent space to Kendall's shape space (Bookstein, '96; Walker, '96). The images of each specimen were recorded with a Hi8 (Hitachi) camcorder. Images were digitized using the Snappy Video Snapshot (Play Inc., version 2.01; Rancho Cordova, California). A total of 14 landmarks were collected on 82 specimens (stan-
The nonuniform component was computed using the uniform component in addition to variability explained by the regression model. Shape change, the additional percentage of components in determining overall size-related growth trajectory was obtained by plotting the principal component scores against centroid size. Finally, the uniform and the nonuniform shape components (U1, shearing, and U2, stretching along the major axis of the consensus configuration) were found. The other columns represent more localized shape components (nonuniform shape components). No information contained in the original landmark configurations is lost at this step except that about centroid size, which can be analyzed independently, and translation and rotation, which have no biological meaning.

To compute the growth trajectories, the weight matrix was used in a relative warp analysis, which is the analogue of a principal component analysis for this kind of data (Rohlf, '93). When significant correlation with centroid size was found, the relative warp scores plotted against centroid size represented the growth trajectory for both the nonuniform and the uniform components of shape change. The associated shape change was visualized as splines relative to the extreme values of the relative warp axis. The growth trajectory and the associated shape change (splines) were then computed for the nonuniform component only via a relative warp analysis of all the columns of the weight matrix except the last two (nonuniform shape components). No information contained in the original landmark configurations is lost at this step except that about centroid size, which can be analyzed independently, and translation and rotation, which have no biological meaning.

To have an estimate of the relative weight of the uniform and the nonuniform components in determining overall size-related shape change, the additional percentage of variability explained by the regression model using the uniform component in addition to the nonuniform component was computed as follows (Rohlf, personal communication). If v is the percentage of variance explained by the uniform and the nonuniform shape components, and nu is the percentage explained by the nonuniform shape component only, then:

\[ u = 100 - (nu \times \frac{100}{v}) \]

where u is the additional percentage of variance explained by the uniform component.

The percentages v and nu are easily computed from the report file of the software TpsRegrw (F.J. Rohlf, State University of New York, Stony Brook, NY). The morphometric softwares cited were implemented by F.J. Rohlf and are available at http://life.bio.sunysb.edu/morph.

RESULTS

Visual observation

Scuba visual observation of D. vulgaris provided data that individuals up to a standard length of approximately 15 mm were found in mid-depth (data on 885 individuals). From this size and larger, they start to settle on the bottom. All individuals from a standard length of approximately 35 mm and up were all found on boulder substrates.

Geometric morphometrics

Figure 3 shows the scatter of residuals at each landmark relative to the consensus configuration after the superimposition with the generalized least-square method. Shape variability is found primarily at landmarks 2, 8, and 9, whereas the tail regions seems to be more homogeneous in shape.

Figure 4 shows the sea bream growth trajectory concerning the overall shape change (uniform and nonuniform) for the size interval considered. The correlation between centroid size and the first relative warp is highly significant (r = 0.8867, P > 0.0001). The pattern of the scattering resembles the saturating growth trajectory described by Alberch and coworkers (Alberch et al., '79): the rate of shape change is high for small sizes and decreases during growth. This decrease starts at centroid size values of approximately 35 mm (standard length ~28 mm). At this stage, there is also an apparent discontinuity in the distribution. The splines relative to the extreme values of the first relative warp (35.4% of the overall shape variability) are plotted at the bottom left (negative values) and upper right (positive values) of the figure. The consensus configuration is positioned corresponding to relative warp 1 value of 0. The most evident

standard length 11.2–82.8 mm) with the software TpsDig (F.J. Rohlf, State University of New York, Stony Brook, NY) (Fig. 2). All landmark configurations were superimposed on a consensus (mean) configuration with a generalized least-square fitting (Rohlf and Slice, '90; Rohlf and Marcus, '93). Size was computed as centroid size (the square root of the sum of squared distances from each landmark to the specimen's centroid). Residuals from the superimposition were modeled by using the thin-plate spline interpolating function (Bookstein, '91). The parameters of the fitted function represent the new set of variables that are contained in a new matrix, the weight matrix. Each row of the weight matrix corresponds to an individual, and each column to a new variable. The last two columns of the weight matrix are the uniform shape components (U1, shearing, and U2, stretching along the major axis of the consensus configuration). The other columns represent more localized shape components (nonuniform shape components). No information contained in the original landmark configurations is lost at this step except that about centroid size, which can be analyzed independently, and translation and rotation, which have no biological meaning.

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characteristic of the allometric shape change of the two-banded sea bream is the stretching along the dorsoventral axis. Such uniform shape change seems to overshadow other more subtle and localized shape changes that are taken into account by further analyses (summarized in Fig. 6). Figure 5 describes shape variability along relative warp 2, which accounts for 11.06% of size-related shape variability and is not correlated with centroid size. It is reported to denote the high variability in shape of the small two-banded sea breams. Variability in small individuals (standard length 11.2–14 mm) is associated with the pelvic fin insertion (landmark 9), the upward displacement of the insertion of the dorsal fin (landmark 2), and head allometry, which, given its independence from size, might not be considered growth allometry but static allometry (Klingenberg, '96).

In Fig. 6, the nonuniform growth trajectory is reported in the form of relative warp 1 plotted onto centroid size. Correlation is highly significant \( r = 0.862, P < 0.0001 \), and such trajectory is very similar to the saturating growth trajectory shown in Fig. 4: again, the rate of shape change is high for small sizes and decreases during growth. As in the previous plot, there is a discontinuity in the distribution of relative warp scores for the nonuniform component as well. The major nonuniform shape changes indicated by the splines can be summarized as a negative allometry of the head region and an expansion of the anterior body region (defined by landmarks 2, 3, 8, and 9) both along and perpendicular to the anteroposterior axis. The latter is driven by the upward displacement of landmark 2 (insertion of the dorsal fin). The base of the anal fin (landmarks 7 and 8) is characterized by a negative allometry. The tip of the mouth (landmark 1) is displaced ventrally in larger individuals. The peduncular region is relatively narrower in larger individuals.

Figure 7 shows, for completeness, the relationship between uniform shape change and centroid size (uniform growth trajectory): the correlation between the two is highly significant \( r = 0.848, P < 0.0001 \). The uniform component (stretching and/or shearing) adds an additional 62.77% to the variance explained by the regression model. Splines at the top and bottom of the figure show how the uniform shape changes in the
observed size range involve an overall broadening along the dorsoventral axis.

DISCUSSION

Because of major changes in ecology, size, and morphology during its ontogeny and growth, the two-banded sea bream represents an appropriate biological material for the study of ecomorphological relationships (Norton et al., '95). Size-related shape changes during the early juvenile stages of D. vulgaris seem to follow a precise pattern.

Fig. 4. Growth trajectory for both the uniform and the nonuniform components of shape change. Splines at the top and the bottom of the figure show the size-related shape change. The consensus configuration corresponds to a relative warp 1 (RW1) value of 0.

Fig. 5. Shape variability as summarized by relative warp 2 (RW2).
Changes are very rapid for small sizes and decrease with growth up to an apparently stable stage. Early juveniles have a streamlined body shape typical of pelagic larvae and acquire a rounded shape suitable for maneuvering (Webb, '84) as adults (Stoner and Livingstone, '84).

The rate of this shape change is high, suggesting the need for a rapid morphological shift. The steep portion of the growth trajectory corresponds to the size range in which the habitat transition occurs (Harmelin-Vivien et al., '95; Tunesi et al., '97); the trajectory dramatically changes its slope at

![Fig. 6. Nonuniform growth trajectory. Splines at the top and the bottom of the figure show the nonuniform shape change occurring during growth. RW1, relative warp 1.](image1)

![Fig. 7. Uniform growth trajectory. Splines at the top and the bottom of the figure show the uniform shape change occurring during growth. PC1-principal component 1.](image2)
a standard length of approximately 28 mm, roughly the size at which settlement and the successive phase of dispersion have been observed in the area of study. The growth trajectories reported closely reflect a saturating growth curve. This is considered to be the result of feedback mechanisms that determine the end of allometric growth (Alberch et al., '79, p. 303). The trajectory might be interpreted as well as a two stage growth curve (Bookstein, '91, p. 355): the first stage is characterized by a dramatic morphological change for a small size interval, and the second by a change in size not accompanied by a change in shape (isometry).

The transition from the pelagic to the nectobenthic life is considered one of the most critical periods of the life cycle of the genus Diplodus and a crucial phase for the success of recruitment (Garcia-Rubies and MacPherson, '95). A rapid change in shape might witness the need to quickly acquire the shape features suited for a nectobenthic life.

The shape changes observed in D. vulgaris appear in fact to be related to the changing ecology of the species. In small individuals, a streamlined body shape (study of the uniform component), a relatively large peduncle (study of the nonuniform component), and a rounded head (study of the nonuniform component) are characteristics that are typical for fishes that swim and feed in the water column (Lindsey, '78; Winemiller, '90). The streamlined shape of small juveniles might also be a consequence of the rapid increase in total length in the postlarval stages, which are to escape the viscous forces imposed by their low Reynolds's number (Muller and Videler, '96). The broad profile of the larger juveniles and the narrowing of the peduncle correspond to some of the characteristics of the typical maneuver described by Webb ('84) and Ehlinger ('90) and are shape features that allow for quick starts and rapid turns in complex environments. Motta and coworkers (Motta et al., '95) relate these characteristics to an epibenthic type of feeding in which food particles are found on the substrate. The subterminal displacement of the tip of the mouth observed in larger juveniles of D. vulgaris might evidence this change in diet, which is known to characterize the habitat transition of the species (Brothers and McFarland, '81). Figure 8 shows the difference in mouth position between small and large juveniles, as well as the changing shape of the head. The posterior displacement of the anterior insertion of the anal fin, which corresponds to the position of the anus, might witness an elongation of the intestine. In fish, this is generally related to the transi-

Fig. 8. Diplodus vulgaris. Head region of the 20-mm juvenile (left) and the 80-mm juvenile (right).
tion from a carnivorous to an omnivorous diet. Such a transition has actually been observed in D. vulgaris (Porcile et al., '89).

Moreover, the higher morphological variability in smaller D. vulgaris organisms is in accordance with the observations made by Kozhara ('88) and Loy et al. ('96) on the high morphological variability of juvenile cyprinids relative to subadult and adult specimens. According to Kozhara, high variability in juveniles can be the result of selection acting and expanding the norm of reaction, i.e., the phenotypic plasticity of a population in response to environmental gradients (Severtsov, '81), thus allowing for deviations from the ontogenetic trajectory. Kozhara concludes that this plasticity in fish might be adaptive.

The study of growth trajectories (Gould, '77; Alberch et al., '79; Atchley, '87), despite its interest, is not sufficiently appreciated in recent literature, probably because of a theoretical deficiency in defining biological forms (the problem of parametrization of Atchley, '87). In this sense, geometric morphometrics can provide the proper framework in which to represent growth and ontogenetic trajectories. One reason for this consists in the attention focused on the definition of the variables to be measured, which have to incorporate biological meaning in order to avoid communicating a correct interpretation of results. Linear measures, angles, or morphological indexes used in traditional morphometrics fail in the description of the geometry of forms and are not defined in a rigorous biological framework such as the concept of homology. It is not possible to visualize shape changes. Moreover, these methods do not allow for the study of covariation of parts of the organism, and shape is not defined unambiguously. Thus, they are not suitable in defining a correct morphospace in which results can be interpreted. Homologous landmarks bear information on the geometry of form, are the mathematical basis of the study of deformation, and allow for the biological interpretation of results. The splines directly visualize allometry. Relative warp analysis provides the right space in which to visualize ontogenetic and growth trajectories. This method greatly contributes to the description of the crucial phases of the autecology of D. vulgaris and should be considered a valuable tool in defining morphospaces in the context of ecomorphology and biodiversity studies (Roy and Foote, '97).

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LITERATURE CITED


