Differential correlates of diet and phylogeny on the shape of the premaxilla and anterior tooth in sparid fishes (Perciformes: Sparidae)

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Abstract

We explore the correlational patterns of diet and phylogeny on the shape of the premaxilla and anterior tooth in sparid fishes (Perciformes: Sparidae) from the western Mediterranean Sea. The premaxilla is less variable, and in spite of the presence of species-specific features, a common structural pattern is easily recognizable in all species (i.e. the ascending and the articular processes are fused in a single branch, as in many percoid fishes). In contrast, tooth shape is more variable, and different structural types can be recognized (e.g. canine-like or incisive). Coupling geometric morphometric and comparative methods we found that the relationship between shape, diet and phylogeny also differs between premaxilla and tooth. Thus, the shape of the premaxilla is significantly correlated with food type, whereas the shape of the teeth is not correlated with diet, and probably reflects the species phylogenetic relationships. Two biological roles, resistance against compressive forces generated in the buccal cavity and the size of the oral gape, would explain the ecomorphological patterns of the premaxilla. The premaxilla and anterior tooth appear to evolve at different rates (mosaic evolution) and represent an example of morphological traits belonging to the same functional unit but following uncoupled evolutionary pathways.

Introduction

The adaptive character of a morphological structure (i.e. a cause-and-effect relationship between shape and environmental forces) is often not easily demonstrable because of two sources of uncertainty. Namely, (1) the lack of an appropriate working hypothesis relating the morphology of a structure and its biological role in the life of an organism (Bock, 1980) and (2) the existence of phylogenetic inertias masking the expected correlational ecomorphological patterns (Felsenstein, 1985). To overcome the uncertainties in the study of adaptation related to phylogenetic inertia and polarity of character change, it is therefore important to use the background of a phylogeny to bridge an observed pattern of morphologi-

cal variation with the hypothesized underlying adaptive process (Coddington, 1988, 1990).

In fishes, the diversity of forms displayed by the mouth anatomy has drawn the attention of those interested in biological adaptation. Thus, the interface between shape and prey use have been extensively described (e.g. Keast & Webb, 1966; Alexander, 1967, 1970; De Martini, 1969; Chao & Musick, 1977; Liem, 1978, 1979, 1980; De Silva *et al.*, 1980; Yamaoka, 1982; Lauder, 1983; Lauder & Clark, 1984; Motta, 1989; Wikramanayake, 1990; Wesneat, 1994; Motta *et al.*, 1995; Winemiller *et al.*, 1995).

We analyse the feeding apparatus of 14 sparid fishes with the aim of testing the existence of a significant correlation between the shape of two structures belonging to the same functional unit (premaxilla and anterior tooth) and some food features. Herein we take advantage of the well established morphological knowledge of feeding apparatus to formulate a working hypothesis of jaw ecomorphology, and of inferring a reliable

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phylogenetic hypothesis of the species considered based on analysis of DNA sequences. We have coupled geometric morphometric methods (Rohlf & Marcus, 1993) with comparative methods (Rohlf, 2001a) to get a better understanding and interpretation not only of the change of shape, but also of the links between a structure and some selective forces (prey properties) that may orientate future works aimed at ascertaining the adaptive nature of fish jaws.

Materials and methods

Data acquisition

The trophic morphology of 14 species of sparid fishes (Table 1) was explored through the analysis of the premaxilla and its anterior dentition. The jaws were dissected from adult specimens. Images of 132 premaxilla and 108 teeth were captured utilizing a video camera (Microm-ECV, Microm España SA, Barcelona, Spain) with a macro-objective (Sigma, Sigma Corporation, Tokyo, Japan). Images were digitized using Optimas. The labial view of the left premaxilla was captured and an outline was traced following the margin of the bone. As the anterior teeth of the labial row were the most diversified, the first tooth of this row was selected for the analysis of the dentition. In some species, the labial row presented some conical teeth slightly enlarged before the more developed teeth; in these cases, the first of the larger ones was chosen. A frontal view image of each tooth was captured and the contour of its shaft was drawn, closing the curve with a straight line at the level of the incision between the pedicle and the shaft.

X and *Y* coordinates of 100 equidistant points for each outline were determined using tpsDig 1.31 (Rohlf, 2001b). For each outline, the coordinates of two *land-*
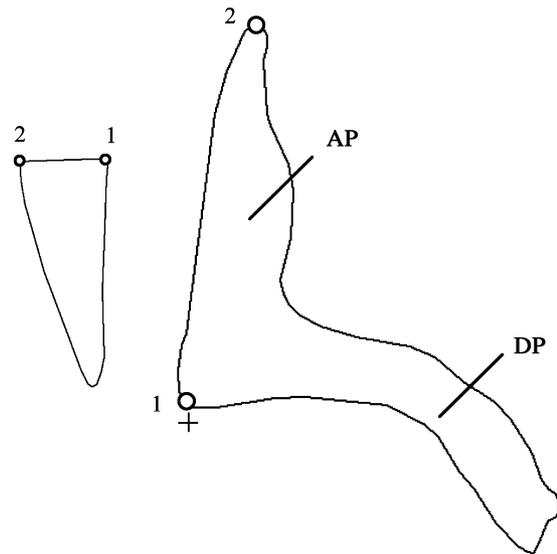

Fig. 1 Landmarks (1 and 2) and outline for tooth and left premaxilla. DP, descending process; AP, ascending process.

marks (geometrically homologous points) were also recorded (Fig. 1). The axis defined by these two landmarks was used to re-orientate all the specimens to a common axis (abscissa axis). The objects were then scaled by setting the *centroid size* (Bookstein, 1991) to the unit.

Shape description

The parameters estimated adjusting the 100 points to an Elliptic Fourier function (Kuhl & Giardina, 1982) were treated as morphological variables that define the shape of the taxa. The outlines were well recovered by the

Table 1 List of species studied and sample sizes for premaxilla and tooth. Accession numbers for genetic markers used for phylogenetic reconstruction are indicated.

Species	Acronym	Sample size		Accession number	
		Premaxilla	Tooth	COI	16S
Boops boops (Linnaeus, 1758)	Bo_boo	6	6	AJ319810	AJ247268
Dentex dentex (Linnaeus, 1758)	De_den	8	8	AF143197	AJ247271
Diplodus annularis (Linnaeus, 1758)	Di_ann	15	10	AJ277366	AJ247286
Diplodus puntazzo (Cetti, 1777)	Di_pun	10	9	AJ277368	AJ247291
Diplodus sargus (Linnaeus, 1758)	Di_sar	18	13	AJ277369	AJ247293
Diplodus vulgaris (Geoffroy St. Hilaire, 1817)	Di_vul	13	13	AJ277370	AJ247294
Lithognathus mormyrus (Linnaeus, 1758)	Li_mor	4	4	AF240712	AJ247285
Oblada melanura (Linnaeus, 1758)	Ob_mel	6	5	AF240701	AF247399
Pagellus acarne (Risso, 1827)	Pa_aca	10	4	AF240713	AJ247281
Pagellus bogaraveo (Brünnich, 1768)	Pa_bog	5	6	AJ319818	AJ247283
Pagellus erythrinus (Linnaeus, 1758)	Pa_ery	14	9	AJ276881	AJ247284
Pagrus pagrus (Linnaeus, 1758)	Pa_pag	9	8	AF240729	AJ247277
Sarpa salpa (Linnaeus, 1758)	Sa_sal	5	5	AF240704	AJ247269
Sparus aurata (Linnaeus, 1758)	Sp_aur	9	8	AF240735	AJ247279

superposition of 15 harmonics. Two matrixes of 132 and 108 rows (corresponding to the number of specimens analysed for the premaxilla and the teeth, respectively) and 62 columns ($4n + 2$, n = number of harmonics) were computed using NTSYSpc (Rohlf, 1993).

Because of the limited number of pieces that could be analysed relative to the number of morphological variables, a principal component analysis (PCA) based on the variance–covariance matrix was computed to reduce the number of dimensions of the morphospace. The first three PCA axes (explaining 88.6 and 94.4% of variation of premaxilla and tooth, respectively) were retained.

A canonical variate analysis (CVA) was computed on the reduced PCA matrix (i.e. the first three PCA axes) to summarize the variation between species. In the space defined by canonical variates, the species are arranged according to their morphological similarity; the more alike two species are, the shorter is the spatial distance between them. The canonical scores of species centroids (i.e. the mean of the points representing specimens) were used as morphological descriptors for testing the correlation between morphology of feeding apparatus and the trophic ecology of species (see below).

Food classification and feeding habits

Classification of prey in taxonomical units is inadequate for ecomorphological studies and it must be replaced by a classification reflecting the functional demands the prey impose on the predator (Barel, 1983). Among the several food properties that could interact with the organism design (Wikramanayake, 1990; Wesneat, 1994; Norton, 1995; Shoup & Hill, 1997; Sibbing & Nagelkerke, 2001) we analysed those related to the habitat and to the escape response because they could be plausibly related to the general morphological patterns observed in the sparid jaws.

We separated prey into four trophic categories. We divided the benthic prey into 'sessile' prey, a category that included vegetal and sessile animals, which live attached to the substrate (e.g. sponges, adherent bivalves, cirripeds, ascidians, benthic hydrozoans, and bryozoans) and 'mobile benthic' prey, grouping vagile organisms that live in association with the bottom and may utilize the structural complexity of the substrate to avoid predation (e.g. polychaetes, gastropods, bivalves, brachiurids, ophiuroids, echinoids). The pelagic prey were divided into 'nektonic' prey, represented by organisms that move in the water column and actively escape from predators (e.g. cephalopods, fishes), and 'planktonic' prey, category that grouped organisms suspended in the water column (fish eggs and larvae, copepods, salps).

The description of feeding habits compiled from scientific literature was expressed as a function of the food categories described above (Table 2). The use of a quantitative dietary index to characterize the feeding habits of species was not possible because of the lack of unification in the methods employed to describe them and to the fact that only qualitative information was available for some species. Therefore, we used a semi-quantitative classification of percentage scale, allocating only the values 100, 75, 50, 25 and 0%.

Three orthogonal variables describing feeding habits were extracted using principal coordinate analysis (PCoA) of the double-centred euclidean distances matrix obtained from the original semiquantitative variables.

Molecular phylogeny

From a statistical point of view, the species are not independent points because they share characters transmitted through the same phylogenetic lineage, and some analyses based on comparisons of taxa are incorrect (Felsenstein, 1985). The incorporation of phylogeny in

Table 2 Feeding habits of species according to four ecological categories of prey based on habitat and response to escape (fuzzy variables; see text).

Species	Sessile	Mobile benthic	Nektonic	Plancktonic	References
Boops boops	0.5	0	0	0.5	Anato & Ktari (1983), Bell & Harmelin-Vivien (1983)
Dentex dentex	0	0	1	0	Morales-Nin & Moranta (1997)
Diplodus annularis	0.5	0.5	0	0	Bell & Harmelin-Vivien (1983)
Diplodus puntazzo	1	0	0	0	Sala (1996)
Diplodus sargus	1	0	0	0	Sala (1996)
Diplodus vulgaris	0.75	0.25	0	0	Sala (1996)
Lithognathus mormyrus	0	1	0	0	Froglia (1977)
Oblada melanura	0	0.5	0	0.5	Fasola *et al.* (1997)
Pagellus acarne	0	0.5	0.5	0	Domanevskaya & Patokina (1984), Morato *et al.* (2001)
Pagellus bogaraveo	0	0	0.75	0.25	Morato *et al.* (2001)
Pagellus erythrinus	0	0.75	0.25	0	Ghannundi (1980), Ardizzone & Messina (1983), Rosecchi (1983)
Pagrus pagrus	0	0.75	0.25	0	Chakroun-Marzouk & Kartas (1987), Fanlo *et al.* (1993)
Sarpa salpa	1	0	0	0	Verlaque (1985), Antolic *et al.* (1994)
Sparus aurata	0	1	0	0	Suau & López (1976)

comparative studies allows us to resolve the problem of nonindependence of taxa.

All the sparid species selected for our morphometric analyses had sequences of two mitochondrial DNA markers available and accessible through GenBank. These were partial sequences of the cytochrome b gene (Cytb; ~1.1 Kb) and of the large subunit of the mitochondrial rRNA (16S rDNA; ~480 bp). Their corresponding accession numbers are indicated in Table 1.

Sequence alignment for Cytb was trivial, but for 16S rDNA, length differences between homologous fragments required the insertion of alignment gaps in four characters between the positions 200 and 229 in the hypervariable region of the selected ribosomal marker. Three other gaps were required in the positions 297, 351 and 362, none of them ambiguous for the resulting informative positions.

The phylogenetic reconstruction for Sparidae used in subsequent analyses was obtained for the combined matrix of both markers and applying the maximum likelihood criterion in PAUP* 4.0b10 (Swofford, 2002). As a measure of support for the nodes, 100 bootstrap pseudo-replicates were performed in PAUP* using the same parameters and tree search strategy outline below (Fig. 2). Previous to phylogenetic reconstruction, the evolutionary model explaining the nucleotide substitution patterns for the genetic marker was obtained using ModelTest 3.06 (Posada & Crandall, 1998). This program assists in selecting the evolutionary model best fitting a

particular set of data by evaluating up to 56 evolutionary models differing in several parameters related to DNA nucleotide substitution dynamics, including nucleotide composition, nucleotide substitution rates, heterogeneity in the rates of substitution along the DNA sequence, and the proportion of invariable sites. The program selects the model and also estimates the parameter values which can be implemented in PAUP* for the maximum likelihood searches. These searches were made heuristic, using a neighbour joining tree as the starting topology for subsequent rearrangements using the TBR algorithm (Swofford, 2002).

The same evolutionary model obtained with ModelTest was used to estimate the genetic distances between pairs of sparid taxa using the 'show pairwise distances' option in PAUP*. This distance matrix was used in phylogenetically based statistical methods.

Phylogenetic inertia

Some methods have been developed to resolve the problem of nonindependence of taxa in comparative biology (Rohlf, 2001a; Blomberg & Garland, 2002; Diniz-Filho & Tòrres, 2002; Martins *et al.*, 2002). Here we use two methods that can be included within the family of generalized linear models (GLM). Phylogenetic eigenvector regression (PVR, Diniz-Filho *et al.*, 1998) derives a number of new variables summarizing phylogenetic distances, and then uses them in a standard (multivariate) linear model. In more detail, these new variables are the principal coordinates (PCoA) on the (double-centred) phylogenetic distance matrix. These new variables are considered as covariables in a linear model from which the response variables are defined by the shape matrix, and the explanatory variables by the matrix describing the feeding habits. This is equivalent to test the partial effect of feeding habits on the shape of a structure (premaxilla and tooth), adjusting for the effects of phylogenetic relatedness. By interchanging the roles of explanatory variables and covariables, it is possible to decompose the variation in the response matrix according to Legendre & Legendre (1998) and ter Braak & Smilauer (1998), but the significance of the fraction explained by phylogeny remains untestable.

Phylogenetic generalized least-squares approach (PGLS, Martins & Hansen, 1996) takes into account the lack of independence of observations by changing the usual identity matrix (used when the observations are fully independent) by an estimation of the expected (phylogenetic) covariance among species (usually under the Brownian motion model, i.e. the amount of change in a trait is proportional to the branch length). In more detail, we used the transformation suggested by Rohlf, 2001a; eqn 20). Both shape and feeding habits matrices are transformed using the eigenanalysis of the phylogenetic covariance matrix.
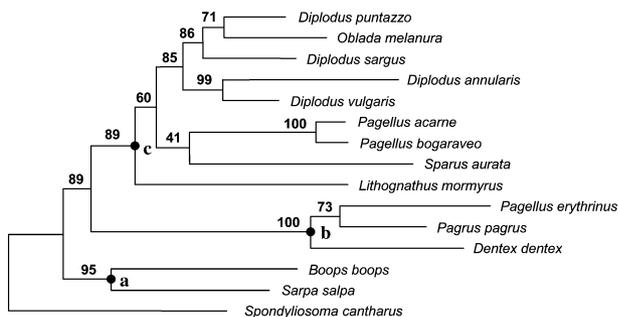

Fig. 2 Maximum likelihood tree of the sampled species of Sparidae based on partial cytochrome b and 16S rDNA sequences rooting the analysis with *Spondyliosoma cantharus*. The implemented evolutionary model, the one best fitting the sequence data as obtained with ModelTest, is a General-Time Reversible (Rodríguez *et al.*, 1990; [A proportion] = 0.262, [C] = 0.314, [G] = 0.169; [A–C rate of change] = 2.006, [AG] = 18.021, [AT] = 4.001, [CG] = 1.001, [CT] = 28.726), with a proportion of invariable sites (I = 0.601) and heterogeneity in the rates of substitution following a gamma distribution with shape parameter $\alpha = 1.177$. The search rendered a single tree with likelihood score $-\ln = 8306.867$. The numbers by the nodes indicate their bootstrap support. Three different lineages were identified on the phylogeny (Hanel & Sturmbauer, 2000): *Sarpa sarpa* and *Boops boops* (a), *Dentex dentex*, *Pagrus pagrus* and *Pagellus erythrinus* (b), and the species of *Diplodus*, *Oblada melanura*, *Pagellus acarne*, *P. bogaraveo*, *Sparus aurata* and *Lithognathus mormyrus* (c).

The final step of testing the (multivariate) effects of feeding habits on shape was common for PVR and PGLS. We used Redundancy Analysis (RDA) that can be interpreted as a multivariate generalization of univariate regression. The analysis finds new uncorrelated variables for two sets of coordinates that explain its maximum variation, with the condition that the corresponding pairs of axes between spaces are maximally correlated. Similarly to other GLM methods, the ratio between the observed and the model-explained variance can be used for testing the significance of the relationship. Here we use the permutation capabilities offered by CANOCO (ter Braak & Smilauer, 1998).

Results

Patterns of shape variation

The morphological raw matrixes were originally composed of 62 harmonics (columns) and the number of specimens (132 rows for premaxilla and 112 rows for tooth). PCAs allowed considerable reduction of the morphospace dimensionality. For both structures, the first three axes extracted by the PCA explained a high percentage of morphological variation. In the case of the premaxilla, the first three principal components explained the 88.6% of the total variance. In decreasing order, these few axes explained 60.3, 23.6 and 4.7% of variation. For the frontal tooth, the principal components one, two and three extracted 94.4% of the variation, and accounted individually for 51.6, 22.9 and 19.9%.

Therefore, only these three first PCA axes were retained for ulterior analyses (i.e. it was considered that they summarize the main patterns of shape variation).

Premaxilla

The CVA of the premaxilla showed the existence of large differences between species (Wilk's Lambda = 5.85×10^{-4}, d.f. (9, 282.5), $P = 10^{-182}$). The first three canonical axes extracted 55.0, 24.7 and 20.4% of the explained variance (Table 3).

Table 3 Results from canonical variate analysis applied to reduced morphological matrixes (after principal component analysis on the 62 variables obtained from Elliptic Fourier analysis).

Canonical vector	Eigenvalue	% Explained variance
Premaxilla		
1	19.73	54.9
2	8.89	24.7
3	7.33	20.4
Tooth		
1	36.90	70.2
2	15.38	29.3
3	0.25	0.5

The ordination of taxa in the tridimensional morphospace formed by the canonical axes is shown in Fig. 3. The species are represented by the mean value of the tridimensional cloud formed by specimens in the canonical space (i.e. the *centroid*). Affinities of species appear uncorrelated with their phylogenetic relationships. Species from the same lineages were segregated along the canonical vectors. There were morphological differences between related species, especially in the lineage c, whereas species with different phylogenetic pathways showed some degree of similarity in the shape of their jaws.

The method described by Monti *et al.* (2001) allows the reconstruction of the shape corresponding to any point located in the canonical morphospace. In this way, it permits visualization of the morphological patterns described by each of the canonical axes, facilitating the interpretation of species ordination. The reconstructed outlines corresponding to the maximum and minimum value for each canonical variable are shown in Fig. 4. The two extreme outlines of one axis were superimposed to facilitate the interpretation of morphological changes. The first axis principally expressed differences in width, length and disposition of the descending process (DP). Higher values correspond to a premaxilla provided with a narrow and elongated DP, with its longitudinal axis and the anterior edge of the ascending process (AP) forming an obtuse angle. Lower values correspond to a premaxilla showing processes about the same size, forming an acute angle, and a broader DP.

The major morphological difference between the configuration of maximum and minimum values of the
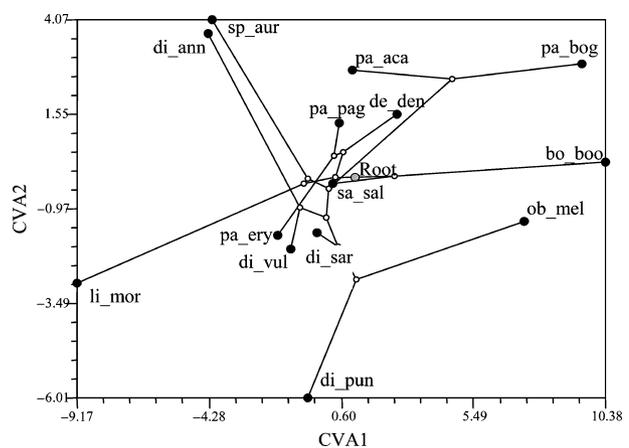

Fig. 3 Species ordination in the canonical space formed by the first and second axes according the shape of their premaxilla. The phylogenetic tree (Fig. 2) is superimposed to evidence the phylogenetic relationships between species. The position of the internal nodes was approximated using COMPARE (Martins, 2003), assuming no intraspecific variability and a Brownian motion model of character evolution. The ancestral state was determined independently for each of the CVA axes.
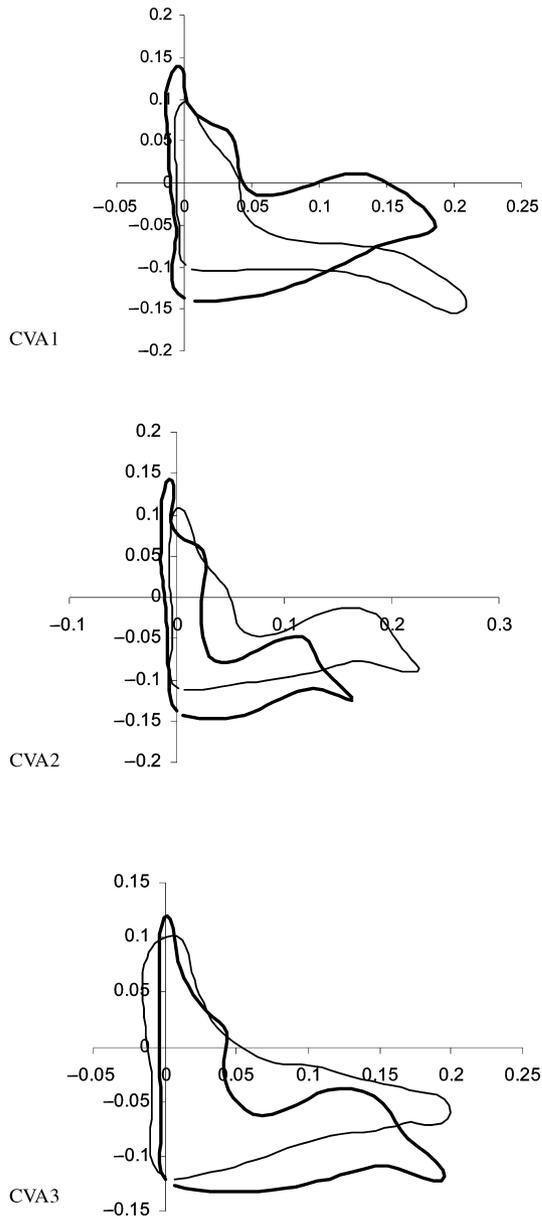
Fig. 4 Morphological patterns of premaxilla described by first (top), second (centre) and third (bottom) canonical axes of the canonical variate analysis. The thinner line corresponds to the maximum value of the axis and the thicker line corresponds to the minimum value.

second vector was localized in the relative length of the processes. Higher values coincide with a premaxilla that has a DP more elongated than the AP. As values get closer to the minimum, the DP gets shortened and the AP prolonged.

The third axis indicates differences in width of the AP and the body region. The maximum value corresponds to a wide premaxilla at the level of the body and AP regions, and an AP with a rounded tip. The minimum value
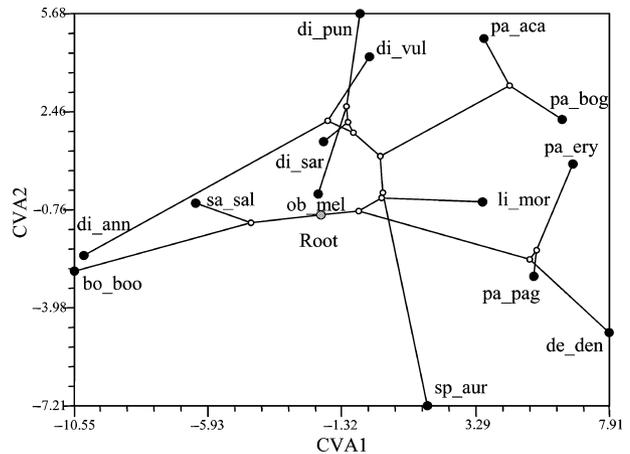

Fig. 5 Species ordination in the canonical space formed by the first and second axes according the shape of their teeth. The phylogenetic tree (Fig. 2) is superimposed to evidence the phylogenetic relationships between species.

represents a premaxilla with a narrower body region and an AP enlarged and sharp-pointed.

Anterior tooth
The CVA of teeth showed that differences between species were large and highly significant (Wilk's Lambda = 1.29×10^{-3}, d.f. (9, 224.1), $P = 10^{-127}$). The first two canonical axes combined explained an elevated percentage of total variation (99.53%). The percentage of the variance extracted by the third axis was low (0.5%) (Table 3).

There was some concordance in the morphological relationships with respect to the phylogeny of the group: the species were arranged according to their lineages (Fig. 5), with the lineage a mainly placed on the left of the morphospace, the lineage b on the right, and the lineage c localized on an intermediate position (Fig. 5). A morphological convergence was observed in tooth shape between *Boops boops* and *Diplodus annularis*. Both species have short, wider and vertically disposed incisor-like teeth, however they feed on different prey types.

The morphological patterns of teeth are indicated in Fig. 6. The first axis showed a morphological transformation from an incisor with wide and short shaft to an elongated caniniform tooth. The second axis expressed a morphological shift ranging between a rough canine, thick and round-pointed, to a chisel-type incisor, narrow on its base and enlarged near the crown.

Ecomorphological patterns

The comparative methods used here can be included within the family of GLM. PVR transforms the phylogenetic distance matrix (D) into a set of eigenvectors, called phylogenetic eigenvectors by applying a PCoA. The first three factors explained 71.5% of variation (43.7,
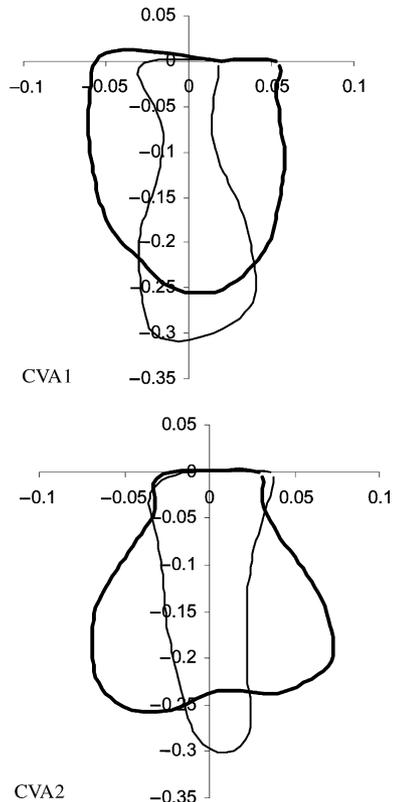
Fig. 6 Morphological patterns of teeth described by first (top) and second (bottom) canonical axes of the canonical variate analysis. The thinner line corresponds to the maximum value of the axis, and the thicker line corresponds to the minimum value.

Table 4 Phylogenetic eigenvector regression: variance partitioning and results of Monte Carlo test (1999 iterations) corresponding to a Redundancy Analysis between premaxilla and tooth shape (response variable) and explanatory variables (diet and phylogenetic matrices).

Explanatory variables	Covariable	F	P-value	Explained variance (total variance = 1)
Premaxilla				
Phylogeny + diet	–	3.263	n.t.	0.737
Phylogeny	Diet	0.862	n.t.	0.097
Diet	Phylogeny	5.046	0.002	0.570
Tooth				
Phylogeny + diet	–	4.906	n.t.	0.808
Phylogeny	Diet	3.233	n.t.	0.266
Diet	Phylogeny	1.488	0.240	0.122

Null hypothesis: no correlation between structure shape and explanatory variables.
n.t., Not testable.

17.2 and 10.6%, respectively). The degree of correlation between the matrix D (after double-centring) and the matrix of euclidean distances in the space defined by the first three eigenvectors was high ($r = -0.771$) and statistically significant ($z = -9.2615$, $P < 0.001$). These phylogenetic eigenvectors were considered as variables in the following RDA.

For the premaxilla, the RDA model considered both feeding habits and phylogeny as explanatory variables. Note, however, that the only fraction testable is the effect of feeding habits. Accordingly, complete variance partitioning is detailed in Table 4, but only the P-values corresponding to the effects of feeding habits are indicated. The explanatory variables combined retained 73.7% of the morphological variation. According to the results of partial RDAs (pRDA, RDA with covariables) there was a significant correlation between the form of the premaxilla and the trophic ecology ($F = 5.046$, $P < 0.01$), after removing the effect of phylogeny on phenotype (i.e. employing phylogenetic variables as covariables in the regression analysis). The ecological variables explained 57% of morphological variance.

In the shape-diet pRDA, the first two axes explained 68.2% of variance associated to the ecological variables. The third vector only added 0.2% to the previous percentage. The first two canonical axes were highly correlated ($r = 0.953$ and $r = 0.709$, respectively) (Table 5).

In the case of teeth, the explanatory variables accounted for 80.8% of variation in shape. However, the partition of the explained variance obtained from pRDAs revealed that there was no statistically significant correlation between tooth shape and feeding habits when phylogenetic inertia was removed ($F = 1.488$, n.s.). The phylogenetic variables retained 26.6% of explained variation (Table 4).

In the partial ordination of tooth morphology and phylogenetic affinities, the two first vectors explained 57.5% of variation associated to phylogeny; the third axis explained only 0.6%. The correlation coefficients between the first two canonical axes were 0.837 and 0.522, respectively (Table 5).

The ecomorphological correlations for premaxilla and feeding habits are shown as a triplot (Fig. 7; ter Braak & Smilauer, 1998). The angle between vectors indicates their correlation (a perpendicular angle indicates no correlation between variables). Their lengths indicate the magnitude of influence of each variable on the canonical axis (large vectors indicate more influential variables). Species that feed principally on pelagic prey showed jaws with high values of the morphological variable cva1, specially those species that feed on plankton, and in contrast, species that feed principally on benthic prey showed lower values of the morphological variable cva1. Species that feed on nektonic prey presented high values of the morphological variable cva2, whereas species feeding on sessile prey presented lower values for this variable. We would like to emphasize here the utility of geometric methods to

Table 5 Phylogenetic eigenvector regression: relationships between shape and explanatory variables (diet and phylogenetic variables).

Partial RDA	Canonical axes			
	Axis 1	Axis 2	Axis 3	Total
Premaxila				
Shape-phylogeny				
Eigenvalue	0.067	0.028	0.002	
Correlation between axes	0.715	0.621	0.112	
% Explained variance	18.7	7.7	0.6	27.0
Shape-diet				
Eigenvalue	0.486	0.082	0.002	
Correlation between axes	0.953	0.709	0.116	
% Explained variance	58.3	9.9	0.2	68.4
Tooth				
Shape-phylogeny				
Eigenvalue	0.228	0.035	0.003	
Correlation between axes	0.837	0.522	0.876	
% Explained variance	49.7	7.8	0.6	58.1
Shape-diet				
Eigenvalue	0.113	0.009	0.000	
Correlation between axes	0.692	0.353	0.105	
% Explained variance	35.9	3.0	0.0	38.9

RDA, Redundancy Analysis.

interpret the morphological meaning of the canonical axes (Figs 4 and 6).

The corresponding triplot for tooth shape is omitted as there was no significant ecomorphological pattern relating tooth morphology and diet.

The results achieved by PGLS, the other comparative method applied, are essentially the same as those obtained by PVR (Table 6). The shape of the premaxilla was found to be significantly correlated with feeding habits ($P < 0.0005$). Conversely, the correlation between tooth shape and feeding habits was not significant.

Discussion

Main ecomorphological patterns

Morphological jaw variation among Mediterranean sparid fishes can be explained by both phylogeny and diet. However, there were differential correlates of these factors on the two features analysed (premaxilla and anterior tooth).

According to the ecomorphological patterns obtained, the shape of the premaxilla is mainly related to prey habitat. The main differences were principally found in the breadth of the toothed limb. The species that feed on pelagic prey tend to have a thinner jaw with a narrower toothed limb, especially those species that are plantivores. On the contrary, species that feed principally on the benthos present broad mandibles with a spacious
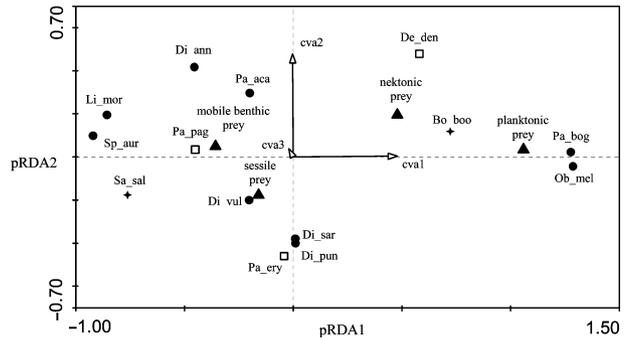

Fig. 7 Triplot corresponding to the partial Redundancy Analysis (phylogenetic variables selected as covariables) on the premaxilla shape. Quantitative response variables (morphological variables cva1, cva2 and cva3) are indicated by arrows, and categorical explanatory variables (sessile prey, mobile benthic prey, nektonic prey and planktonic prey) are indicated by triangles. Species with the same symbol belong to the same phylogenetic lineage.

Table 6 Phylogenetic generalized least-squares: results of Monte Carlo test (1999 iterations) corresponding to a Redundancy Analysis between transformed matrices of shape (response variables) and feeding habits (explanatory variables). The applied transformation is based on an eigenanalysis of the phylogenetic covariance matrix between species and it takes into account the nonindependence of observations.

Explanatory variables	*F*	*P*-value	% Variance
Premaxilla			
Feeding habits	5.035	0.0005	69.1
Unexplained			30.9
Tooth			
Feeding habits	1.346	0.2780	37.4
Unexplained			62.6

toothed limb. The second pattern of shape variation seems to be related to the escape response of prey in the following manner: species with a tendency to feed on evasive prey have a larger DP in comparison with species that feed on sessile organisms.

Conversely, tooth shape seems to be independent of feeding habits, with species feeding on similar food items showing different tooth types.

Adaptive character of premaxilla and tooth

In order to understand ecomorphological relationships, one needs to know both the functional changes associated with the morphological pattern of variation and the reasons why certain form–function complexes are more advantageous to counteract the selective forces imposed by prey (Bock & Wahlert, 1965; Wainwright, 1996). The information required is not currently available for sparid

fishes, so at this point, we discuss the ecomorphological patterns described above based on the extensive knowledge of morphological, functional, ecological and behavioural aspects of feeding performance in fishes.

The width of the premaxilla bone might be functionally related with the strength of the jaw against compressive forces. The mandible bones must resist the compressive forces generated in the mouth cavity during feeding, and a stronger bone can be expected to have greater strength (Herring, 1993).

A link between the jaw's robustness and biting strength has been shown in probatocephalus, a sparid fish that feeds on sessile organisms by biting. During growth, as jaw muscles and bones became more massive and the force generated by the oral jaws increases, there is an increment in the capture of sessile hard-shelled prey (Hernandez & Motta, 1997).

Other sparids feed on nonattached prey that can be taken by other feeding methods during their initial stage of development, and they experience a dietary shift when the properties of the feeding apparatus allow them to generate the powerful bites needed to successfully feed on sessile organisms. The morphological changes of the feeding apparatus associated with the increment in the consumption of sessile prey are: (1) an specialized dentition, (2) strong and relatively small jaws, and (3) massive adductor muscles (Vu-Tàn-Tuè, 1964; Christensen, 1978; Stoner & Livingston, 1984; Luczkovich *et al.*, 1995).

The same pattern of covariation of durophagous regimen and trophic morphology was found between populations of two tiger fishes (*Xanthichthys ringens* and *Balistes vetula*). The populations that fed on hard-shelled prey by biting had more massive jaw adductor muscles and bones than the populations that used suction feeding to capture and ingest plankton or soft-bodied benthic invertebrates (Turingan *et al.*, 1995).

The length of the DP determines the size of the oral gap. Then, the second ecomorphological pattern obtained could be translated to words as: species with a tendency to feed on evasive prey have bigger mouths (i.e. larger DP) compared with species that feed on sessile organisms. Piscivorous fishes swallow entire organisms so they are gap-limited predators consuming only prey smaller than their mouths (Hambright, 1991). Thus, one would expect that a large gape might improve capture success of piscivores, which rely on their jaws to catch the prey. Norton (1995) verified that cottids with large mouth showed higher capture success than cottids with smaller mouth when feeding on evasive prey. Kotrschal (1989) observed a general trend towards an increment in the consumption of sessile prey by fishes with strong jaws. The short and robust premaxilla and dentary of these species form strong lever arms that are able to transmit the force exerted by musculature and its strength, improving the ability to tear attached organisms or to cut pieces of larger prey. In contrast to piscivores,

browser fishes uncouple mouth size from prey size, through their ability to bite pieces of larger prey (Luczkovich *et al.*, 1995).

The general ecomorphological model described above appears not to include explicit predictions for the relationship between tooth shape and diet. Some explanations of the lack of similarity in tooth shape between species with similar diets would be: (1) fishes might develop different feeding strategies to feed on the same food category; (2) one tooth type could be useful to perform several tasks; (3) other food properties have been relevant in the evolution of dentition and (4) in some species, teeth have not played an important role in predation.

The later point could be the case of sucking feeders. When fish suck, teeth do not interact with prey and apparently do not perform any task during the predation process, especially when a fish preys on tiny organisms. Plankton-feeding fishes usually prey by suction feeding (O'Brien, 1987) so that it could probably be the feeding behaviour adopted by *Oblada melanura* and *Boops boops* when they feed on planktonic organisms. These species have similar jaws but dissimilar teeth. If there were not selective forces acting upon the teeth when fishes preyed on planktonic organisms, tooth shape would remain more or less unaltered and to some extent would reflect the phylogenetic relatedness, as it is the case with these secondary planktivores.

Planktivore fishes show a tendency to reduce the size and number of teeth, to the point of their disappearance (Davis & Birdsong, 1973). This tendency would be explained by the lack of a biological role of teeth in suction feeders.

In sparids, all the species that feed on benthic prey posses stronger jaws, indicating that they may capture or process the food by the oral jaws:

(1) Species that feed on benthic invertebrates present different types of sharp teeth which differ clearly in their development. Differences in the development of the anterior dentition would be related to differences in the means of food acquisition. For example, the strong teeth of *Sparus aurata* and *Pagrus pagrus* would be useful to firmly grasp or crush their prey, but the reduced teeth of *Lithognathus mormyrus*, *Pagellus erythrinus* and *Pagellus acarne* are probably not useful for biting, so these fishes probably suck loose invertebrates and process them in the hind part of the mouth using the molar teeth.

(2) Consumers of sessile prey have well-developed teeth that differ in shape. Larger, rounded, protruding and robust incisors of *Diplodus sargus* and *D. vulgaris* would be preferentially useful to pick tough invertebrates adhered to the substrate. As shown by Vandewalle *et al.* (1995), *D. sargus* can use their strong incisors to crush hard-shelled prey. Longer, thinner and more protruding incisors as presented by *D. puntazzo* possibly are less useful to crush or firmly grasp and tear

adherent invertebrates. The characteristics of the incisors of *D. puntazzo*, together with the loss of molars, would be a specialization to feed on larger sessile prey, such as algae and sponges. *D. annularis* has short, wider, straight-edged and vertically disposed incisors that resemble those of the sparid *Lagodon rhomboides* described by Stoner & Livingston (1984). As in the case of *L. rhomboides*, the incisors of *D. annularis* would be less suitable to tear organisms firmly attached to the substrate, but effective to cut pieces of larger organisms as seagrasses or polychaetes.

The dentition of *Sarpa salpa* with a unique row of strong and bicuspid incisors, set vertically on jaws with a long root perpendicular to the stalk, would be a dental specialization to cut pieces of larger and tough vegetals, like phanerogams and erect algae. The dentition pattern of *S. salpa* resembles those observed in herbivorous blennioids. The evolutionary transformations of the oral jaws of blennioids may illustrate the trends followed by other acanthopterygian fishes to reach a cutting device (Kotrschal, 1989), and among them, those followed by the herbivorous lineage of sparids, as reflected to some extent along the ontogenetic development of dentition in plant consumers such as *Boops boops* and *S. salpa* (Vu-Tàn-Tuè, 1964; Christensen, 1978).

Species that feed on pelagic prey have elongated jaws and probably feed by less active methods of feeding such as ram or suction feeding:

(1) In the continuum formed by ram and suction feeding, secondary planktivores as *B. boops* and *Oblada melanura* would be positioned near the extreme of the suction method (e.g. coastal planktivores; O'Brien, 1987). These species differ in the shape of the frontal teeth, however both have teeth of reduced size and disposed principally in one row (*B. boops* has only one row of teeth whereas *O. melanura* has some small conical teeth behind the frontal teeth). These fishes present external body characteristics typical of planktivores fishes such as large eyes, short snout and oblique mouth, that seem to be adaptations to feed on tiny organisms (Hobson, 1991).

(2) The piscivorous species *Dentex dentex* would be closer to the extreme of ram feeders, so this method is more adequate to feed on evasive prey (Norton, 1991). *Pagellus bogaraveo* would be positioned in some intermediate point of the ram-suction continuum predating on both nektonic and planktonic organisms.

Evolutionary patterns

The premaxilla and anterior tooth represent a case of mosaic evolution. The jawbone has changed substantially over 400 M.Y. (Shaeffer & Rosen, 1961), during the formation of a protusible mouth. But within the family Sparidae, all species analysed possess the same type of premaxilla (i.e. with the ascending and articular processes united in a single branch). Notwithstanding the apparent 'stability' of the premaxilla, a shape analysis suggests that it continued evolving adaptively to develop new biological roles related to the emergence of a manipulation behaviour (i.e. to resist the compressive forces generated in the mouth cavity). All lineages seem to develop the same response: to increase bone thickness. This fact would imply that phylogenetic relatedness would remain disguised.

On the contrary, teeth would represent an innovative character that had been profoundly modified and could be an important feature in the evolutive radiation of this diverse family (Day, 2002). Other speciose families also show a great variety of tooth types (Kotrschal, 1989). Contrary to premaxilla, species could diverge to develop different biological roles that allow them to feed successfully on specific prey types, decreasing niche overlap. Differences in the selective forces that probably took part during the formation of specialized tooth types seem to complicate the recognition of the adaptive character of dentition. In spite of the divergent evolution of this feature, some directional tendencies should exist during the formation of highly modified dentitions, as it is suggested by the importance of the phylogenetic component on tooth shape.

The jaws of sparid fishes illustrate the evolutionary tendencies of higher teleostean fishes in inshore marine environments. The general pattern shows an improvement of prey manipulation that increases the success in predation on sessile and hard-shelled benthonic prey (Gosline, 1987). However, the morphometric analysis reveals that the same functional unit can be composed of subunits evolving following independent ways. Moreover, in the case studied, slight morphological changes to a structure can represent adaptations to new selective forces, whereas clearly divergent structures can delineate, to some extent, taxonomic relationships.

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