

Relationship between shape and trophic ecology of selected species of Sparids of the Caprolace coastal lagoon (Central Tyrrhenian sea)

Corrado Costa · Stefano Cataudella

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Synopsis The shapes of juveniles of nine species of the family Sparidae (*Diplodus annularis*, *Diplodus puntazzo*, *Diplodus sargus*, *Diplodus vulgaris*, *Lithognathus mormyrus*, *Pagellus acarne*, *Sarpa salpa*, *Sparus aurata*, *Spondyliosoma cantharus*), collected in the tide channel of the Caprolace Lagoon (Central Tyrrhenian Sea—Italy) were studied using geometric morphometry. These species have different ecologies. The trophic ecology of each species, reported as TROPH values, are related to shape. For the first time the relationship between shape and trophic ecology in sparids was studied in a quantitative way giving an ecomorphological meaning to the shape differences. Mean shapes of carnivorous, omnivorous and herbivorous fish were extracted, analyzed and found to be unique. Strict herbivores such as *Sarpa salpa* have a small mouth gap; omnivores such as the four species of the genus *Diplodus* have a higher body (discoidal) and a caudal peduncle shorter and higher; carnivorous species such as *Lithognathus mormyrus*, possess a relatively larger head region, a larger mouth gap, a longer body and a caudal peduncle longer and narrower.

Keywords Ecomorphology · Geometric morphometrics · Feeding habits · Fish ecology · Sparidae

Introduction

According to the framework of ecological morphology the species morphology is related to their ecology. The study of the form of organisms structures in relation to their functions defines the functional morphology domain. Functional morphology tries to explain how the structures of animals' bodies work. It shows how particular designs have been favoured by natural selection because they work better than the alternatives, or are particularly economical or energy or materials (Alexander 1988). At the same time the ecological morphology, which encompasses the functional morphology, defines the study of the form in relation to the species role within its community (Motta et al. 1995a, b). In this sense, ecomorphology is defined as the study of the relationship between environmental factors (physical and biotic) and species form in order to isolate the mutual contribution of one to the other and the reverse (Motta and Kotrschal 1992). In particular, it attempts to understand the relationships existing between the morphological variation among individuals, populations, or species and higher taxa, and the corresponding

C. Costa (✉) · S. Cataudella
Aquaculture and Experimental Ecology Laboratory,
Biology Department, University of Rome Tor
Vergata, Via della Ricerca Scientifica, 00133 Rome,
Italy
e-mail: corrado_costa@libero.it

variation in their ecology (Liesler and Winkler 1985; Sardà et al. 2005).

The link between morphology and diet in fish is provided by feeding performance (Norton 1991; Wainwright 1991; Motta and Kotrschal 1992). As suggested by Wainwright and Richard (1995), morphology shapes diet through its influence on a fish's feeding capability. A major challenge in fish ecology is to establish the linkage between morphology and diet. Functional morphological, biomechanical, and physiological analyses may be used to determine the expected consequences of morphological variation on feeding performance (Wainwright 1988).

The Sparidae are percoid fish with oblong bodies, usually deep and compressed. The head is large, often with a steep upper profile. Snout and supraorbital areas are scale-less. The mouth is often small, with the upper jaw reaching no further than the middle part of the eye. Preoperculum is scaled, without spines on the margin. Colours vary greatly, from silver to reddish to almost black (Nelson 1994). Almost all Sparidae are demersal, and are found in relatively shallow waters, often in rocky areas; the young fish generally live in shallower waters than the adults; fry and fingerling school together, while adults usually show a solitary behaviour, but some species (*Sarpa salpa*) have a schooling behaviour (Nelson 1994). Due to their excellent flesh, many representatives of this family have a high commercial value. The nine species examined have different ecologies (Domanevskaya and Patokina 1984; Mariani et al. 2002; Pita et al. 2002)¹: *Diplodus puntazzo* feeds as a typical grazer on seagrass beds, *D. annularis*, *D. sargus*, *D. vulgaris* and *Spondylisoma cantharus* were found to be generalists and remarkably omnivorous, *Lithognathus mormyrus* behaves as a strict carnivorous soft bottom feeder, *Pagellus acarne* is a predator hunting macrofauna. *Sarpa salpa* is strictly herbivorous grazing on aquatic plants, and *Sparus aurata* is an euryphagous, opportunistic benthic feeder. Also the relationships between dentition and feeding behaviour are well known in this

family (Stoner and Livingston 1984; Hanel and Sturmbauer 2000).

In this study the shapes described by geometric morphometrics (Bookstein 1991; Rohlf and Marcus 1993; Marcus et al. 1996, Dryden and Mardia 1998; Rohlf 2000) were compared with the fractional trophic level (TROPH), described by Stergiou and Karpouzi (2002), and reported by Froese and Pauly (2004)¹, of nine species of juvenile Sparidae collected in the tide channel of the Caprolace lagoon (Central Italy). No study so far has examined the relationship between body form, described with geometric morphometrics, and feeding habit, expressed by the TROPH index (Stergiou and Karpouzi 2002; Froese and Pauly 2004)¹. In other families, lethriniid (Carpenter 1996), gasterosteid (Walker 1996, 1997), serranid (Cavalcanti et al. 1999) and percids (Guill et al. 2003), geometric morphometrics was used to study the general relationship between shape and feeding habit in a qualitative manner. The aforementioned method helps clarify the shape differences linked to feeding habits, an important contribution to ecomorphology.

Materials and methods

A total number of 313 individuals of 9 species of juvenile Sparids was collected in the tide channel of the Caprolace Lagoon (Central Tyrrhenian Sea—Italy). The number of specimen per species, the mean total length (TL), the standard deviation for each measurement, the diet and the TROPH level are reported in Table 1.

An image of each specimen was collected with an Olympus digital camera, RGB 24 bit, with a resolution of 1,600 × 1,200 d.p.i..

Morphometric features can be sampled quickly and precisely by processing digital images (Rohlf 1990). Geometric morphometrics were developed to quantify and visualise deformations of morphometric points (landmarks) in a coordinate space, as conceptualised much earlier by D'Arcy Thompson (1917). Landmarks are defined as homologous points which bear information on the geometry of biological forms (Bookstein 1991).

¹ Froese R, Pauly D (eds) (2004) FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2004).

Table 1 Sample size, mean total length, total length standard deviation, diet and TROPH level

Species	N° Ind.	Mean TL (cm)	St. Dev. TL	Diet	TROPH
<i>Diplodus annularis</i> (DA)	52	11.9	1.4	Algae, crustaceans, gastropods, polychaetes, other	3.21 ± 0.43
<i>Diplodus puntazzo</i> (DP)	36	15.5	1.2	Sponges, algae, anthozoans, other	2.88 ± 0.32
<i>Diplodus sargus</i> (DS)	49	13.7	2.1	Algae, bivalves, gastropods, echinoderms, other	3.02 ± 0.38
<i>Diplodus vulgaris</i> (DV)	49	11.9	0.8	Bivalves, ophiurids, polychaetes, algae, other	3.22 ± 0.34
<i>Lithognathus mormyrus</i> (LM)	34	13.5	1.4	Amphipods, decapods, molluscs, gastropods, fish, other	3.44 ± 0.48
<i>Pagellus acarne</i> (PA)	5	10.8	0.7	Decapods, ophiurids, fish, other	3.68 ± 0.56
<i>Sarpa salpa</i> (SS)	45	13.9	1.4	Algae, epiphytes	2.58 ± 0.27
<i>Sparus aurata</i> (SA)	38	16.2	1.0	Molluscs, decapods, annelids, other	3.39 ± 0.49
<i>Spondyliosoma cantharus</i> (SC)	5	15.2	0.9	Mysids, crustaceans	3.27 ± 0.47

Points were digitised using the software TPS-DIGIT² (Rohlf 2004) applied to the left side of each specimen. A total number of 20 landmarks were identified (Fig. 1).

A randomisation test using the software Morphueus (Slice 1998) was performed in order to establish the effect of unequal sample size.

To remove all information unrelated to shape, a generalized orthogonal least-squares Procrustes (GPA) superimposition (translation, scaling and rotation) described in Rohlf and Slice (1990) was conducted on the sets of landmarks. A consensus configuration was computed. Shape variables termed ‘partial warps’ were computed by comparing each specimen to this consensus configuration, and variation in these shape variables was summarised by relative warp analysis, analogous to a principle component analysis of the partial warps³ (software TPSrelw; Rohlf 2003a)³. The consensus configuration for each species was visualised by ‘unwarping’ the images of each specimen so that the landmarks coincide with

their positions in a reference configuration using the software TPSsuper (Rohlf 2003b)⁴.

Even if Procrustes superimposition removes isometric effects of size, the allometric effects of size (i.e., a change in shape with size; Loy et al. 2001), that may remain, was eliminated using individuals with the same size range.

Residuals from the fitting were modelled with the thin-plate spline interpolating function (for a complete coverage of the geometric morphometric techniques see Rohlf and Bookstein 1990; Rohlf and Slice 1990; Bookstein 1991; Marcus et al. 1996; Dryden and Mardia 1998; Rohlf 2000).

To explore the overall within-sample shape variability, relative warp analysis (RWA), analogous to a principal component analysis for these kinds of data, was performed (using the software TPSrelw; Rohlf 2003a)³. This method quantifies change in shape, and patterns of morphometric variations within- and among-groups can be quantified if each individual is considered to deviate from an ‘average’ shape, namely the consensus configuration (Cadrin 2000). The splines (deformation grids) of the extremes of each axis was visualised using the software TPSrelw (Rohlf 2003a)³.

² Rohlf FJ (2004) TpsDig, ver. 1.40. Dept. of Ecology and Evolution, State Univ. of New York at Stony Brook, Stony Brook.

³ Rohlf FJ (2003a) TpsRelw, ver. 1.31. Dept. of Ecology and Evolution, State Univ. of New York at Stony Brook, Stony Brook.

⁴ Rohlf FJ (2003b) Tps Super, ver. 1.12. Dept. of Ecology and Evolution, State Univ. of New York at Stony Brook, Stony Brook.

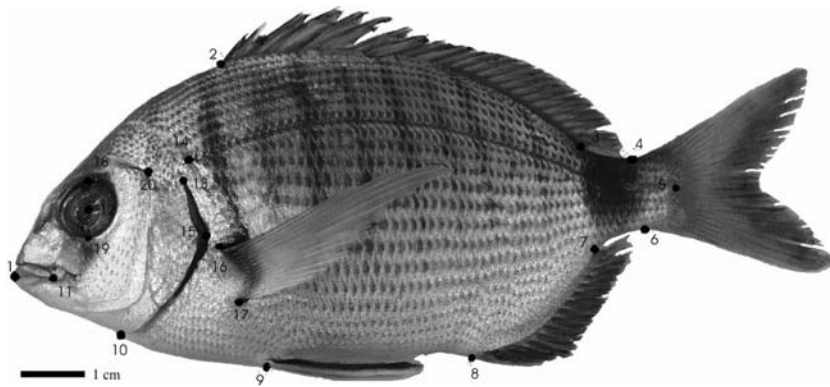


Fig. 1 Landmark's description (*Diplodus sargus* in the example): (1) snout tip; (2) and (3) anterior and posterior insertion of the dorsal fin; (4) and (6) points of maximum curvature of the peduncle; (5) posterior body extremity; (7) and (8) posterior and anterior insertion of the anal fin; (9) insertion of the pelvic fin; (10) insertion of the operculum on the lateral profile; (11) posterior extremity

The mean value for each species on each RWA axis was related to the TROPH value for each species reported by Froese and Pauly (2004)¹ (Table 1). The significance of this correlation for each axis was tested with Spearman's cross-correlation.

TROPHs were calculated for each dataset based on the full array of prey items in the diet as presented in the original studies. TROPH expresses the position of organisms within the food webs that largely define aquatic ecosystems (Pauly and Palomares 2000). Real consumers do not usually have TROPHs with integer values and the definition of TROPH for any consumer species (*i*) is (Pauly and Palomares 2000; Stergiou and Karpouzi 2002):

$$\text{TROPH}_i = 1 + \sum_{j=1}^G \text{DC}_{ij} * \text{TROPH}_j$$

where TROPH_j is the fractional trophic level of prey (*j*), DC_{ij} represents the fraction of *j* in the diet of *i* and *G* is the total number of prey species. Thus defined, the TROPH of fish species could be classified, as suggested by Stergiou and Karpouzi (2002) using the following functional trophic groups: (a) pure herbivores ($\text{TROPH} = 2.0\text{--}2.1$, mean = 2.02, SD = 0.03) which feed on red, brown, green and bluegreen algae; (b) omnivores with a preference for vegetable material

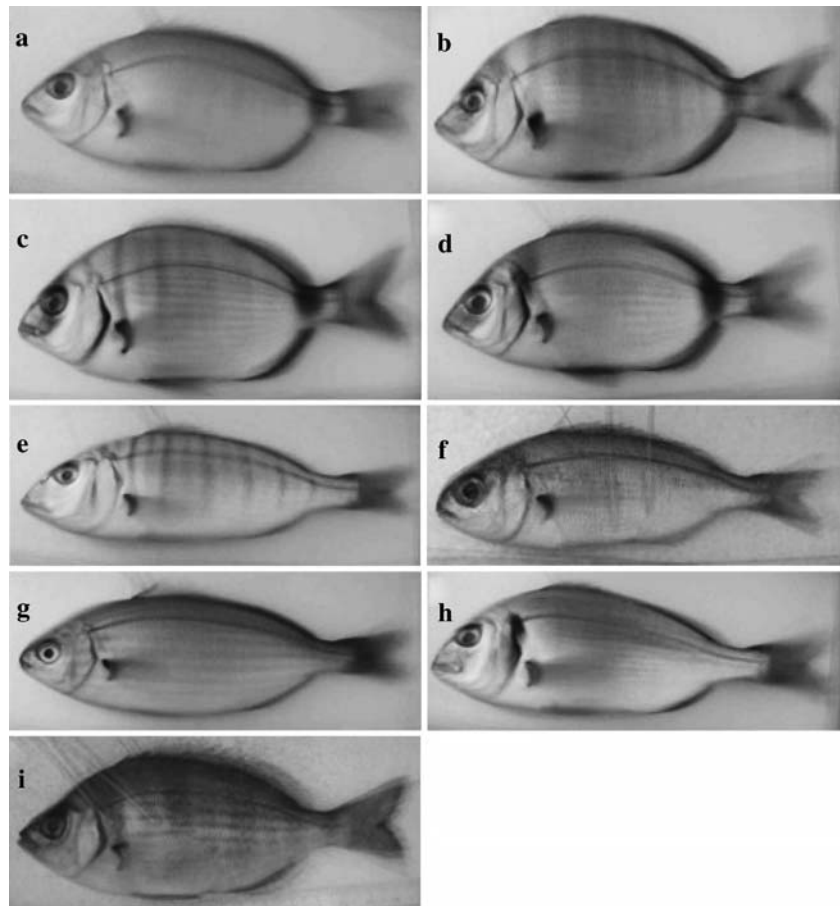
of premaxillar; (12) centre of the eye; (13) superior insertion of operculum; (14) beginning of the lateral line; (15) point of maximum extension of operculum on the lateral profile; (16) and (17) superior and inferior insertion of the pectoral fin; (18) and (19) superior and inferior margin of the eye; (20) superior margin of the preoperculum

($2.1 < \text{TROPH} < 2.9$, mean = 2.5, SD = 0.12), but also capable of feeding on other prey, such as sponges, hydrozoans, anthozoans, polychaetes, ostracods, isopods, amphipods and copepods; (c) omnivores with a preference for animal material ($2.9 < \text{TROPH} < 3.7$, mean = 3.4, SD = 0.19) but feeding on a wide variety of prey (e.g., algae, foraminifera, brachyurans, balanoids, ascidians, amphipods, appendicularians, annelids, isopods, gastropods, cnidarians, ophiurids, polychaetes, cladocerans, mysids, euphausiids, fish larvae, cephalopods); and (d) carnivores with a preference for large decapods, cephalopods and fish ($3.7 < \text{TROPH} < 4.5$). The diets of the 9 species of sparids studied in this work are reported in Table 1.

Results

Randomisation tests between pairs of species using the software Morpheus (Slice 1998) showed that in only four cases out of 36 randomisation tests the null hypothesis, i.e., identical shapes, was not rejected, whereas all the remaining comparisons were significant ($0.01 < P < 0.05$). Two sets of species, *Pagellus acarne*, *Diplodus annularis*, *D. sargus* and *D. vulgaris* and *Spondylisoma cantharus* and *Sarpa salpa* had shapes that were statistically identical. This is possibly due to the

Fig. 2 Consensus configuration of the nine species obtained with the software TPSsuper: (a) *Diplodus annularis*; (b) *Diplodus puntazzo*; (c) *Diplodus sargus*; (d) *Diplodus vulgaris*; (e) *Lithognathus mormyrus*; (f) *Pagellus acarne*; (g) *Sarpa salpa*; (h) *Sparus aurata*; (i) *Spondyliosoma cantharus*



lower number of individuals of *Pagellus acarne* and *Spondyliosoma cantharus* examined. For this reason the shape differences in these four cases will be always be rejected.

Figure 2 illustrates the consensus configuration of the nine species obtained with the software TPSsuper (Rohlf 2003b)⁴. In these average images, those areas that appear fuzzy or ‘out of focus’: correspond to those parts of the images that vary from specimen to specimen in a way that is not well correlated with the variation in the positions of the landmarks. This is an optimal instrument to identify the real shape of each species eliminating the inter-individual variation.

Figure 3 shows the regression between the first two axes of the Relative Warp Analysis (RW1 and RW2). These two axes account for 39.58% and 21.05% of the variance respectively. It is possible to observe three different clusters.

Group I comprises *Lithognathus mormyrus* at the negative extreme as well as *Sparus aurata* and *Pagellus acarne*. Group II is comprised of the four species of the genus *Diplodus* and *Spondyliosoma cantharus*. *Sarpa salpa* (Group III) is separated from the other species. The splines of the extreme values of RW1 (on the right side of Fig. 3), separate oblong shapes (negative values), from discoid shapes (positive values). Splines of the extreme values of RW2, are shown on the bottom side of Fig. 3. It is possible to observe that the spline on the negative side of RW2 axis, correspond to fish that have a relatively larger head region, a larger mouth gap, a longer body and a longer and narrower caudal peduncle.

The mean shape of each group, extracted with TPSsuper (Rohlf 2003b)⁴, is shown in Fig. 4. Also in this case the superimposition eliminate the inter-group variations increasing the common characteristics described above.

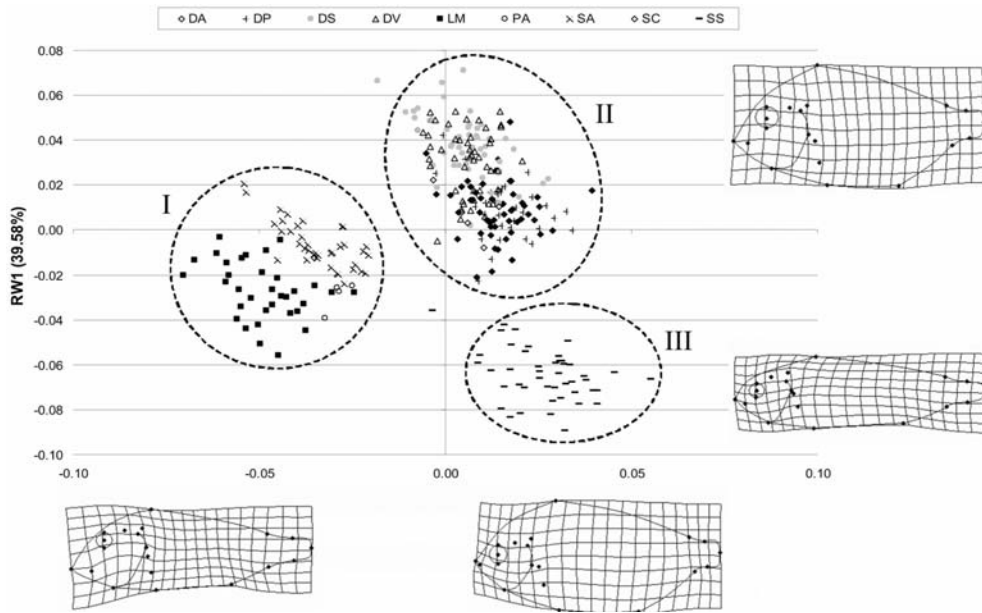


Fig. 3 Relative Warp Analysis: plot of the first two axes. On the right side: splines relative to the extremes of the first axis of the RWA. On the bottom side: Splines relative to the extremes of the second axis of the RWA

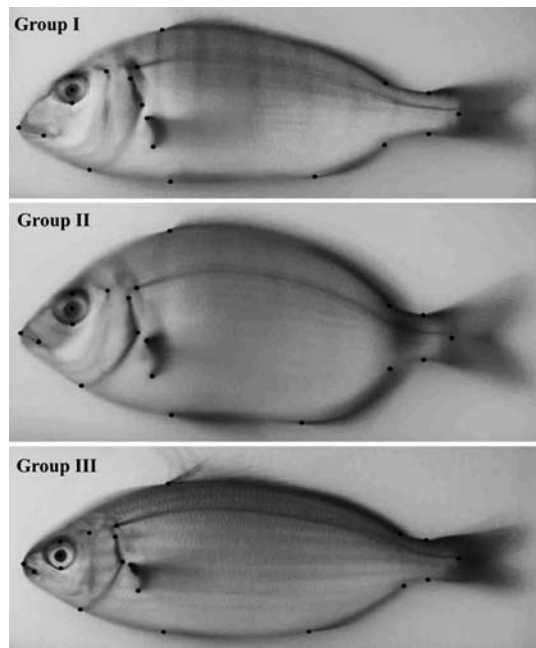


Fig. 4 Mean configuration of the three group obtained by the RWA: Group I *Sparus aurata*, *Lithognathus mormyrus* and *Pagellus acarne*; Group II *Diplodus annularis*,

Diplodus puntazzo, *Diplodus sargus*, *Diplodus vulgaris* and *Spondyliosoma cantharus*; Group III *Sarpa salpa* (Group III)

The correlation between the mean value for each species on each RWA axis and the TROPH value for each species reported by Froese and Pauly (2004)¹ (Table 1), tested with Spearman's

cross-correlation shows a significant ($P < 0.05$) correlation only for RW2 (Spearman r value = -0.8666 ; $P = 0.002$) (Fig 5). Regression values are reported Fig. 4.

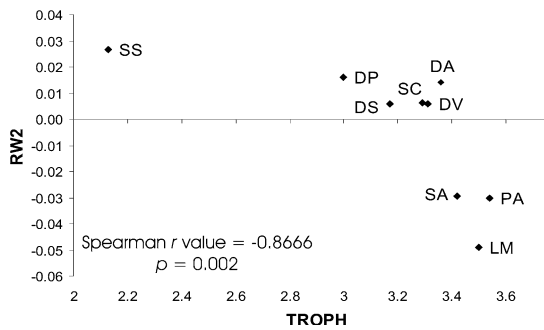


Fig. 5 Regression between RW2 and TROPH values for each species

Discussion

Ecomorphology is based on the hypothesis that the functional design of an organism is linked to its ecology (Cutwa and Turingan 2000). Inter-specific, ecomorphological studies exist in the ichthyological literature (Luczkovich et al. 1995; Kassam et al. 2004). For the first time, in this study, we examined quantitatively the relationship between feeding habits and body shape morphology among different species of the same family, Sparidae. These species have different ecologies and settle on different habitats.

As concluded by Loy et al. (2001) shape differences between 3 sparids of the genus *Diplodus* juveniles appear to be related to ecological differences in their ecology. Also Ruber and Adams (2002) studied the variation in body shape and trophic morphology in several genetic lineages of eretmodine cichlids from Lake Tanganyika linking body shape differences with tooth types. Webb (1984) showed evidence that body shape is a reliable indicator of the swimming behaviour habitat choice and so the ecology of finfish; modern actinopterygian fishes concentrate lateral movements towards the posterior half to third of the body, which further improves thrust and efficiency (Lighthill 1975). In this work RWA shows three different clusters of shape that are correlated also with trophic habits of the nine species of Sparids.

Strict herbivores (group III; Fig. 4c) such as *Sarpa salpa* have a small mouth gap; omnivores such as the four species of the genus *Diplodus* (group II; Fig. 4b) have a higher body (discoidal) and a caudal peduncle shorter and higher;

carnivorous species (group I; Fig. 4a) such as *Lithognathus mormyrus*, possess a relatively larger head region, a larger mouth gap, a longer body and a caudal peduncle longer and narrower.

The omnivorous and herbivorous shape of species of group II and III correspond to some of those characters described by Lindsey (1978) for a carangiform swimmer and studied and classified by Webb (1984). Among undulatory swimmers, the carangiform pattern with little more than half a wave within the body length as described by Breder (1926). Some authors (Webb 1988; Ehlinger 1990; Loy et al. 2001) associate this shape with maneuvering fish that possess shape features that allow for quick starts and rapid turns in complex environments such as reef or rocky shores. Those species are excellent at feeding on a sessile resource. Motta et al. (1995a) relate these characteristics to an epibenthic type of feeding, in which food particles are found on the substrate. For species with these shape features it is possible to eat algae and invertebrates that colonise the sediment. Increased manoeuvring does not mean the sacrifice of a good regular swimming efficiency, however.

The shape of predators (group I) could be classified as subcarangiform (Palomares 1991). This shape retains more of a wave within the body length but concentrating increases in amplitude towards the tail. Subcarangiformes swimmers are presumed to be less efficient and powerful than carangiform swimmers. This shape is associated by Winemiller (1991) to species that possess a trophic behaviour involved in the search of dispersed prey. This is the shape characteristic of species that hunt by sight.

For the first time the relationship between shape and trophic ecology in sparids was studied in a quantitative way giving an ecomorphological meaning to shape differences. Geometric morphometrics and TROPH values are significantly related. Future development of this kind of studies on species of different groups with different ecology could enlarge and quantify the differences of functional design in relation with ecology.

In summary, the present study analyzed shape differences of species with different trophic ecology. Under this limitation that allowed us to extremes shape differences, the present study

successfully discriminated herbivorous, omnivorous and carnivorous sparid models. The morphological features of species are shaped also by other ecological factors than trophic alone. In this sense, species are a mosaic of character where only some of them are shaped by the trophic level. For this reason the geometric morphometric approach is a valid standard tool for the study of the relationship between the shape and other non-TROPH variables such as habitat use (Motta et al. 1995a; Svanbaeck and Ekloev 2003; Kassam et al. 2004), activity, motility (Blake 1983), swimming morphology (Lindsey 1978). This kind of study could contribute to the sinecology of sparids and of fishes in general, further explaining the relationship between shape and ecology.

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