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Feeding ecomorphology of seven demersal marine fish species in the Mexican Pacific Ocean

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Abstract How fish functional morphology shapes species co-existence and assemblage diversity patterns is a fundamental issue in ecological research. In fishes, much is known about the ecomorphological relationships of feeding morphology in coral reef fishes and in freshwater taxa inhabiting distinct environments. However, little is known about the patterns and processes shaping morphological variation in other oceanic taxa; particularly those inhabiting soft bottom habitats. In this study, we assessed patterns of feeding ecomorphology in seven demersal teleost species associated with soft bottoms of the continental shelf in the central Mexican Pacific Ocean. Feeding analyses indicated that some species groups shared similar diets. Likewise, patterns of morphological variation based on geometric morphometrics demonstrated that some taxa did not differ in body shape, while patterns of variation in other species were seen in body length and height, caudal peduncle height and the anal fin anterior insertion point. A multivariate association between diet composition data and overall body shape indicated significant ecomorphological relationships, describing a continuum between species displaying benthopelagic morphology and specializing on prey with high speed swimming ability (Engraulidae), versus species with benthic morphology and specializing on fast escape prey (crustacea). The clear ecomorphological patterns observed for these seven species at both the individual and species levels imply that environmental conditions and resource availability allow these taxa to differentially inhabit and

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exploit the soft bottom ecosystem. Fish diversity is principally represented by the benthic morphology, although benthopelagic morphology, also show a high degree of success in this environment.

Keywords Demersal marine fish · Ecomorphology · Functional ecology · Geometric morphometrics · Trophic ecology

Introduction

The structure of a community of coexisting species may be described by the positions of these species along different resource dimensions of ecological space. These positions depend on the availability of resources and on ecological processes such as interspecific competition or predation (Pianka 1969; Ross 1986; Adite and Winemiller 1997). Whenever interspecific competition predominates, evolution produces non-random assemblages of interacting species, specialized to exploit specific resources according to their morphological, behavioural and physiological characteristics (Sibbing et al. 1994; Motta et al. 1995a, b). Resource partitioning is an important mechanism that enables competing species to coexist (Schoener 1974; Guedes and Araújo 2008). Through evolutionary processes, resource partitioning by competing species can be facilitated by morphological divergence (Taper and Case 1985; Motta and Kotrschal 1992; Nagelkerke et al. 1995).

This simultaneous morphological and ecological segregation illustrates the close relationship between morphology and ecology (Watson and Balon 1984; Winemiller 1991a; Norton et al. 1995). There have been various attempts to conceptualize the interactions between morphology and ecology (Bock and von Wahlert 1965; Barel 1983; Liem 1990, 1993; Motta and Kotrschal 1992; Bock 1994; Reilly and Wainwright 1994; Motta et al. 1995a, b; Smirnov et al. 1995). One approach used in previous studies was to compare morphological variation with variation in ecological characters, either at the intra- or interspecific levels. Together with this inductive comparative approach, functional studies were needed to provide a plausible mechanism for an observed ecomorphological correlation, and thereby generate predictions of the role of morphological variation in determining the potential niche (Barel 1983; Norton et al. 1995; Motta et al. 1995a, b).

The clear relationship between form, function and the realized niche requires an integration of ecology, physiology, behavior, morphology and evolution (Norton et al. 1995). However it is difficult to study morphological integration from this holistic perspective, so most studies have focused on understanding the relationship between morphology and one of these aspects. In ecomorphological studies the selected morphological and ecological variables may often obscure existing relationships because of the confounding influence of evolutionary history, or because these variables are not relevant to important functional relationships (Norton et al. 1995; Aguilar-Medrano et al. 2011). This can be, at least partly, obviated by selecting a suite of morphological characters, which have demonstrated some functional relevance, or were found important in other studies (Rickefls and Miles 1994; Norton et al. 1995; Ferry-Graham et al. 2008). Also, the selection of functional ecological characters instead of those derived from phylogeny (e.g., prey types by taxa) can help to detect meaningful ecomorphological correlations (Norton et al. 1995).

Prior work on the ecology of the soft bottom fish communities in the central Mexican Pacific Ocean has been limited to descriptions of diet composition at both the intra- and interspecific level (Tripp-Valdez and Arreguin-Sánchez 2009; Navarro-González et al. 2012; Tripp-Valdez et al. 2012). However, considerably less is known about how the morphology of these organisms relates to their feeding habit, and whether an ecomorphological association between feeding morphology and resource use is displayed. In this study we describe the feeding ecomorphology of seven demersal teleost species associated with soft bottoms of the continental shelf of Nayarit (Mexican Pacific). For each species we characterize their trophic ecology through an assessment of their prey items, and quantify patterns of morphological variation using geometric morphometric methods to ask the following questions: 1) Do bottom-dwelling species of the Mexican continental shelf specialize in different food resources? 2) Do species in this assemblage differ in body shape? and 3) Is there an ecomorphological association between trophic ecology and body shape in these species?

Materials and methods

The study area is located on the continental shelf of Nayarit (central Mexican Pacific) (Fig. 1). This is a

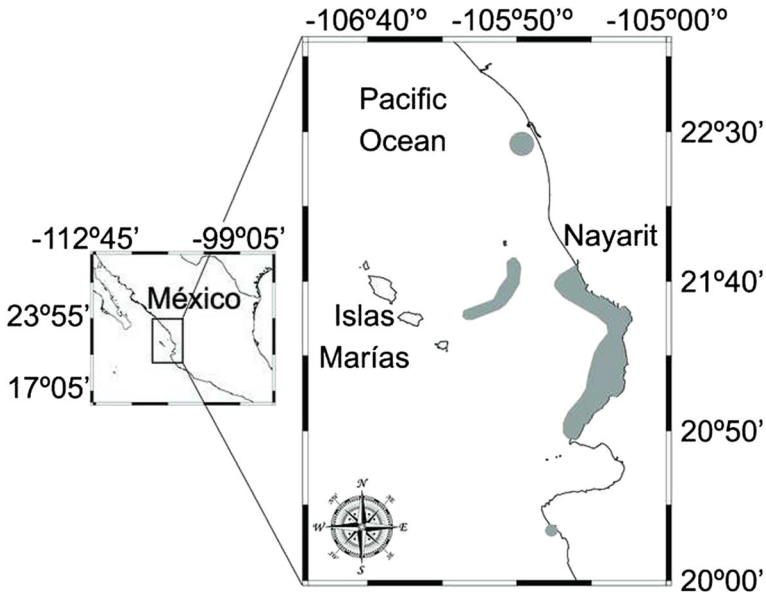


Fig. 1 Study area in the continental shelf of Nayarit (Mexican Pacific). The shadow areas are equivalent to the trawling zones

broad region with a moderate slope, whose primary habitat consists of soft bottoms of terrigenous and coastal sources. A large lagoon and estuarine systems, tidal channels, marshes, wetlands and large rivers that provide high levels of sediment, organic matter, and nutrients (Amezcua 1996) influence the area.

Sampling procedures

Samples were collected from commercial shrimp trawling fisheries, and were obtained from September 2005 to March 2006. These samples were collected at distances from 2 to 36 km from the coast, and at depths between 10 and 76 m (Fig. 1). The sampling adhered to the legal requirements of Mexico. From the samples, fishes were identified taxonomically, were weighed (g), total length (mm) was measured, and digital images of their left lateral side were taken. Additionally, the stomach of each individual was removed and frozen for further laboratory analysis. For subsequent analysis, only adult organisms were taken into consideration (sample sizes are detailed in supplementary material 1; Table S1).

Trophic analysis

In the laboratory, the prey items in each stomach were counted, weighed (mg), and identified to the lowest taxonomic level possible, using specialized faunal guides for the region. Prey that were sufficiently well digested to preclude identification to lower taxonomic levels (e.g., *Engraulis mordax*) were classified at the highest taxonomic level that could be identified (e.g., Teleostei). Diet composition analyses were carried out with all taxonomic levels such that 1) we would not lose important information on specific prey consumed, and 2) so as not to lose potentially significant fractions of unidentified prey in our descriptions.

The ichthyofauna reported during the shrimp fishing season 2005–2006 of the continental shelf of Nayarit included 134 taxa grouped into two classes (Actinopterygii and Chondrichthyes), 18 orders, 53 families and 104 genera (following Nelson 2006). However, only the stomach contents of 31 taxa were sampled. These taxa were chosen because they were the most abundant in the samples, and their body forms could be readily compared using the morphometric protocol described below. In total, 1295 stomachs were analyzed but we restricted our analyses to taxa completely identified to species. To avoid possible biases due to empty stomachs, we worked only with species for which more than 30 individuals had prey items.

Of the 31 total fish taxa considered, we carefully examined seven Perciform species (Supplementary material 1; Fig. S1), which represented some of the most abundant teleosts in this habitat. These were *Selene peruviana* (Guichenot, 1866), *Lutjanus guttatus* (Steindachner, 1869), *Orthopristis chalceus* (Günther, 1864), *Pomadasys panamensis* (Steindachner, 1876),

Centropomus robalito (Jordan and Gilbert, 1882), *Pseudupeneus grandisquamis* (Gill, 1863) and *Polydactylus opercularis* (Gill, 1863).

Rarefaction curve estimates of the number of individuals for which the asymptote of this curve was obtained (Ferry and Cailliet 1996) was treated as the minimal sample size required to adequately describe the species' diet. Additionally, we constructed a mean cumulative diversity curve based on the Shannon-Wiener index, and randomly permuted (500 times) the order of individuals included in the analysis in Matlab (script included in supplementary material 2) (MathWorks 2008). To determine if the cumulative curve reached an asymptote, we compared the slope generated from the curve endpoints to a line of zero slope (horizontal asymptote). To do this, we used the last four mean diversity values of the curve and conducted a linear regression to determine if the slope of the corresponding best fit line was significantly different than a line of zero slope. Using a *Student t*-test we compared the slopes, thus with *P-values*>0.05, the slopes were not significantly different demonstrating that the curve reached an asymptote (Bizarro et al. 2007). Additionally, we calculated the coefficient of variation (CV=(standard deviation (SD) / $\overline{X}$) * 100 %) of the endpoints as a standard precision measure (Bizarro et al. 2007).

To quantitatively describe the diet of each species we used numerical (% N), gravimetric (% W) and frequency of occurrence (% FO) indices, which were included in a tri-dimensional graphic to analyze trophic strategies. This graphic allows for the determination of dominant or rare prey items, generalists or specialists predators and homogeneous or heterogeneous diets (see Cortés 1997). To facilitate comparison among studies we also calculated the percent index of relative importance (%IRI), which is an estimate of the relative importance of the prey (Cortés 1997). We then used permutational MANOVA (1000 permutations) using distances matrices (formerly known as non-parametric MANOVA) (Anderson 2001; Oksanen et al. 2014) to determine whether the trophic resource use differed among pairs of species, with these pairwise comparisons assessed statistically at an experiment-wise α=0.05 using a Bonferroni correction (Bland and Altman 1995; Legendre and Legendre 1998). All analyses were performed in R (R Development Core Team 2014) and tri-dimensional graphs were constructed using SigmaPlot (Systat Software Inc 2008).

Morphological analysis

We used landmark-based geometric morphometric methods (Bookstein 1991; Rohlf and Marcus 1993; Adams et al. 2013) to quantify overall fish shape. With these methods, the shapes of anatomical structures are quantified using the coordinates of homologous locations, after the effects of nonshape variation are mathematically held constant. An important advantage of this approach is that shape information from landmarks, as well as points along curves and surfaces can be included in the same analysis (points on curves and surfaces are termed semi-landmarks, see Bookstein 1997; Bookstein et al. 1999; Gunz et al. 2005). Together, these provide a more complete description of shape, and thus a more rigorous quantitative comparison of the external anatomy of organisms.

In this study, we quantified body shape from images of the left-lateral side of 277 specimens. For each we digitized 16 landmarks and 13 semi-landmarks (Fig. 2) using TpsDig2 (Rohlf 2013a). Next, we performed a generalized Procrustes analysis (GPA: Rohlf and Slice 1990), which translated all specimens to a common location, scaled them to unit centroid size, and optimally rotated them using a least-squares criterion. During this process, semi-landmarks were permitted to slide along their tangent directions so as to minimize the bending energy between each specimen and the overall reference (see e.g., Bookstein et al. 1999). From the aligned specimens, shape variables in Kendall's tangent space were obtained as partial warp scores and the standard uniform components, which were used in subsequent statistical analyses. All morphometric analyses were performed in TpsRelw (Rohlf 2013b).

We used MANOVA to determine whether body shape differed among species. Subsequently, we obtained pairwise Euclidean (Procrustes) distances between the least-squares means of each species, and assessed pairwise shape divergence using a permutation procedure (10,000). With this approach, individuals were randomly shuffled into species groups, least-squares means for each species were obtained, and the set of Euclidean distances from this random assignment of individuals to groups was compared to the observed Euclidean distances (see Collyer and Adams 2007; Adams and Collyer 2007, 2009). Significance levels were evaluated after Bonferroni adjustment.

Finally, principal components analysis (PCA) was used to provide a graphical depiction of patterns of shape variation in tangent space, and thin-plate spline

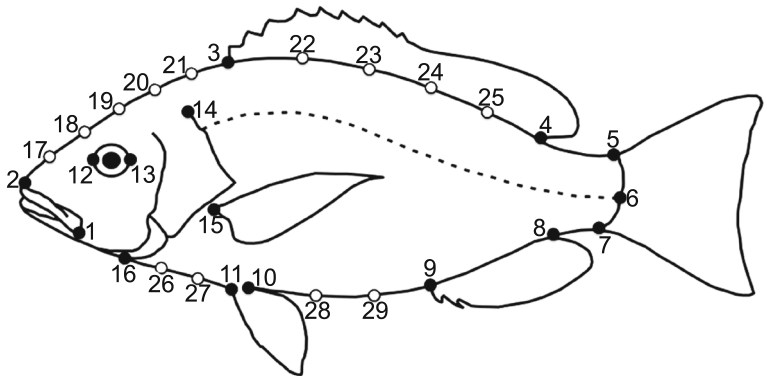


Fig. 2 Position of the 16 landmarks (*dark circles*) and the 13 semi-landmarks (*open circles*) (*ex. Lutjanus guttatus*): 1) posterior edge of superior jaw, 2) snout tip, 3) and 4) anterior and posterior insertion of the dorsal fin, 5) and 7) dorsal and ventral insertion of the caudal fin, 6) end of lateral line, 8) and 9) posterior and anterior insertion of anal fin, 10) and 11) posterior and anterior insertion of pelvic fin, 12) and 13) anterior and posterior edge of the eye, 14) superior insertion of operculum, 15) superior insertion of the pectoral fin, 16) ventral insertion of operculum on the lateral profile, 17) to 21) points on the edge of the body between landmarks 2 and 3, 22) to 25) points on the edge of the body between landmarks 3 and 4, 26) and 27) points on the edge of the body between landmarks 16 and 11, 28) and 29) points on the edge of the body between landmarks 10 and 9

deformation grids (Bookstein 1991) were employed to visually describe the shape differences between species. All analyses were conducted in R (R Development Core Team 2014) and TpsRelw (Rohlf 2013b).

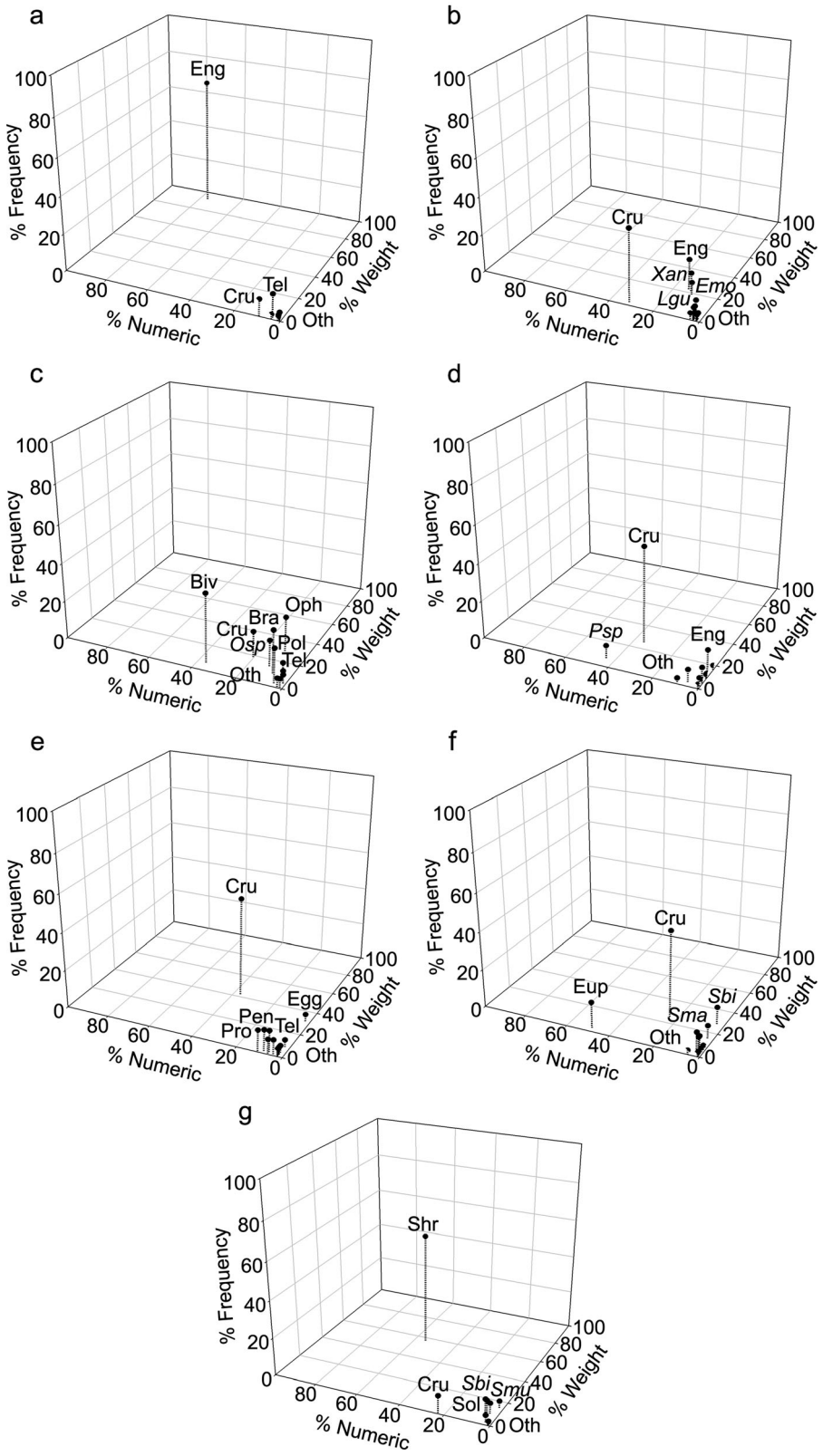
Feeding ecomorphology

We used several approaches to assess the degree of association between morphology and trophic ecology. First, we used a Mantel test (Mantel 1967) to assess species-level patterns of association. Here, we used the Euclidean distances between the least-squares means of each species to represent differences in body shape, and Euclidean distances based on the gravimetric and numerical information of the food preferences to represent trophic ecology. The association between these two distance matrices was then obtained, and statistically assessed using 1000 permutations. Second, the relationship between morphology and trophic ecology based on Euclidean distances between species means was assessed using regression. At the individual level, we determined the extent to which an ecomorphological relationship was displayed between body shape and trophic ecology using Partial Least Squares (PLS) (e.g., Rohlf and Corti 2000; Adams 2004; Arif et al. 2007). Here, the covariation between the matrix of shape variables for all specimens and the matrix of trophic data for all specimens was calculated, and used to determine the degree of association between the two sets of variables. All ecomorphological analyses were performed in R software (R Development Core Team 2014).

Results

Trophic analysis

Cumulative prey curves for all species reached the asymptote indicating sufficient sample size for the diet description, with low variability at the end points (< 2 %) (Supplementary material 1; Fig S2, Table S2). Results of our diet analysis (Supplementary material 1; Table S3) confirmed earlier findings suggesting that these species are generalist predators (e.g., Cortés 1997). The exception to this pattern was *Selene peruviana,* which displayed a more restricted and homogeneous diet (Fig. 3a). For two species (*S. peruviana* and *Lutjanus guttatus*), the engraulid (*Engraulis mordax*) represented the most prevalent prey item in their diets. *Selene peruviana* also preyed upon other fish species and on crustaceans, but in smaller relative proportions to *E. mordax*. The diet of *L. guttatus* contained various teleost species, as well as crabs of the family Xanthidae (Fig. 3b). The diet of *O. chalceus* consisted of five different taxa (echinoderms, brachyuran, polychaetes, teleosts and molluscs), with bivalves representing the most important prey type in terms of %IRI, %N and %FO, while ophiuroid echinoderms were the dominant prey item by weight (%W), and bivalves were the most abundant prey item numerically (Fig. 3c). In contrast, *P. opercularis* preyed primary on shrimp, particularly of the genus *Processa* in terms of %IRI and %N, while engraulid teleosts represented the greatest contribution in terms of %W and %FO (Fig. 3d). The diet of *P. grandisquamis* consisted mainly of crustaceans, with


a
% Frequency
% Numeric
% Weight
Eng
Tel
Cru
Oth
b
Cru
Eng
Xan
Emo
Lgu
Oth
c
Biv
Oph
Bra
Cru
Osp
Pol
Tel
Oth
d
Cru
Psp
Eng
Oth
e
Cru
Egg
Pen
Pro
Tel
Oth
f
Cru
Eup
Sbi
Sma
Oth
g
Shr
Cru
Sbi
Smu
Sol
Oth

◀ **Fig. 3** 3D graphs that relate the trophic indexes for each species [numeric (abundance), weight (biomass) and ocurrence frequency]. a) *Selene peruviana*, b) *Lutjanus guttatus*, c) *Orthopristis chalceus*, d) *Polydactylus opercularis*, e) *Pseudupeneus grandisquamis,* f) *Pomadasys panamensis*, g) *Centropomus robalito*. Abreviations: Pol: Polychaeta, Oph: Ophiuroidea, *Osp*: *Ophiura* spp., Biv: Bivalvia, Cru: Crustacea, Eup: Euphausidae, Bra: Brachyura, Xan: Xanthidae, Shr: Shrimps, Pen: Penaeidae, Sol: Solenoceridae, *Smu*: *Solenocera mutator*, Pro: Processidae, *Psp*: *Processa* spp., *Sbi*: *Squilla biformis*, *Sma*: *Squilla mantoidea*, Tel: Teleostei, *Emo*: *Engraulis mordax*, *Lgu*: *Lutjanus guttatus*, Egg: Fish eggs, Oth: Others

the families Processidae, Penaeidae and Ogyrididae representing the dominant prey items (Fig. 3e). *Pomadasys panamensis* consumed a higher number and more frequently euphausiids, while *Squilla biformis* and *S. mantoidea* stood out for their gravimetric contribution (Fig. 3f). Finally, the diet of *C. robalito* was dominated by shrimp, particularly from the Solenoceridae and Penaeidae families, and from the stomatopod *Squilla biformis* (Fig. 3g).

Using pairwise permutational MANOVA, we found that many species differed significantly in their diets, both in terms of the numerical abundance of prey items (F=6.3167, P<0.001; Table 1) as well as in their gravimetric indices (F=9.3641, P<0.001; Table 2). In terms of numerical abundance, the diet of *C. robalito* differed most from the other species, with the exception of *P. grandisquamis,* whose diet was not significantly different from that of *C. robalito.* In contrast, *L. guttatus* exhibited a diet whose composition was similar to that of all other species except *C. robalito* (Table 1). When diets were examined gravimetrically, *C. robalito* and *S. peruviana* were most distinct, and most of the other species did not differ significantly in their diets (Table 2).

Morphological analysis

Using MANOVA we found significant differences in body shape among species (Wilks'λ=7.704e-11, F= 267.42, P<0.0001). Further, pairwise comparisons based on least-squares means revealed that nearly all species were distinct from one another in terms of body shape (Table 3). The sole exception to this pattern was found with *P. panamensis,* who did not differ in body shape from either *L. guttatus* or *O. chalceus.* These statistical findings were reflected in patterns of shape variation as revealed in the principal components plot (PC1: 63.36 %, PC2: 10.40 %) (Fig. 4), where each species displayed a tight scatter of within-species shape variation relative to between species variability. Here, *S. peruviana, P. opercularis,* and *C. robalito* were most distinct in body shape, and to a lesser extent *P. grandisquamis.* By contrast, *O. chalceus, L. guttatus,* and *P. panamensis* overlapped considerably along the two principal components (Fig. 4).

When viewed using thin-plate spline deformation grids, these patterns of body shape similarity and differences among species were visually confirmed (Fig. 5). Here, *S. peruviana* was characterized as displaying a body shape defined by a flattened and high frontal region, a short and high body and high dorsal outline and low ventral midline. Additionally the ventral contour of the caudal peduncle is above the consensus configuration, while the anal fin is elongated and has a steep slope (Fig. 5). This corresponded generally to a body shape typical of more pelagic species. By contrast, *C. robalito* and *P. opercularis* exhibited a more benthic phenotype, characterized by a broader caudle peduncle, a more fusiform body, and a more terminal mouth (Figs. 4 and 5).

Table 1 Pairwise non parametric MANOVA from the numeric matrix

Species	*C.robalito*	*L.guttatus*	*O.chalceus*	*P.grandisquamis*	*P.opercularis*	*P.panamensis*	*S.peruviana*
C. robalito		5.5944	7.1344	2.5277	5.2911	4.6681	18.5190
L. guttatus	0.0010		3.0411	1.7996	3.2178	1.7109	7.0790
O. chalceus	< 0.001	0.0010		3.3500	2.6360	2.3337	8.2022
P. grandisquamis	**0.0771**	**0.0691**	0.0010		2.7667	1.5119	9.3209
P. opercularis	0.0010	**0.0090**	**0.0340**	**0.0220**		4.4661	11.0190
P. panamensis	< 0.001	**0.0931**	**0.0721**	**0.1842**	< 0.001		10.3940
S. peruviana	< 0.001	**0.0040**	0.0010	**0.0060**	< 0.001	0.0010	

F-values are above the diagonal and *p*-values are below

Bold values correspond to those that are not statistically different (Bonferroni=0.0024)

Table 2 Pairwise non parametric MANOVA from the **gravimetric** matrix

Species	*C.robalito*	*L.guttatus*	*O.chalceus*	*P.grandisquamis*	*P.opercularis*	*P.panamensis*	*S.peruviana*
C. robalito		6.6287	7.3491	8.1524	6.7266	11.6243	38.2160
L. guttatus	< 0.001		2.2300	2.6563	3.0349	3.7009	2.2049
O. chalceus	**0.0070**	**0.0410**		1.3919	2.0836	4.8035	23.4152
P. grandisquamis	0.0020	**0.0060**	**0.0501**		1.6306	1.5265	25.7239
P. opercularis	< 0.001	**0.0030**	**0.1391**	**0.1391**		3.1205	24.0827
P. panamensis	0.0010	< 0.001	**0.0080**	**0.1121**	< 0.001		38.6605
S. peruviana	< 0.001	**0.0881**	< 0.001	< 0.001	< 0.001	< 0.001	

F-values are above the diagonal and *p*-values are below

Bold values correspond to those that are not statistically different (Bonferroni=0.0024)

Since the body shape of *S. peruviana* was significant different from the other six species analyzed, we performed an additional analysis to make sure that the inclusion of this species did not skew the shape results of the other species. To do that, we calculated the other six species shape including and excluding *S. peruviana* from the analysis, and compared both resultant data sets with a linear regression, and contrasted both Euclidean distances matrices with a Mantel Test. Results indicated high correlation between both data sets where the linear regression showed a slope close to one (intercept = -0.0008, slope=1.0149) while the Mantel test showed that there were not significant differences between both distance matrices (r=0.9998, P<0.1). Thus, we concluded that the inclusion of *S. peruviana* in the shape analysis do not skew the shape of the other six species.

Feeding ecomorphology

A Mantel test revealed a highly significant association between body shape and trophic ecology at the species level, in terms of both prey abundance (r=0.9381, P=0.004) as well as prey gravimetric indices (r=0.8234, P=0.033). Linear regression analysis confirmed these findings, and showed the association between morphological traits and trophic variables (Fig. 6). Specifically, fish displaying more pelagic characteristics in their body shape contained a greater volume and proportion of teleosts in their diet, while fish displaying a more streamlined body and deeper caudal region preyed more heavily on crustaceans. Likewise, when ecomorphology was examined at the individual level, the partial least squares analysis found a significant relationship between body shape and trophic ecology (Fig. 7), using both prey abundance data (r=0.6062, P=0.001) and prey gravimetric indices (r=0.6317, P=0.001). Summary plots of this relationship (Fig. 7) found that piscivorous fish such as *S. peruviana* were most different in both body shape and feeding ecology from species that specialized more on shrimp (*C. robalito*). By contrast, species whose diets were most diverse were intermediate to these taxa, both in terms of the feeding axis and the morphological axis (Fig. 7). Finally, species generally displayed greater trophic variation as compared to morphological variation. However,

Table 3 Euclidean distance matrix showing *p*-values between each pair of species based on morphometric information

Species	*C.robalito*	*L.guttatus*	*O.chalceus*	*P.grandisquamis*	*P.opercularis*	*P.panamensis*	*S.peruviana*
C. robalito	1	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
L. guttatus	0.0001	1	**0.0077**	0.0001	0.0001	**0.0113**	0.0001
O. chalceus	0.0001	**0.0077**	1	0.0001	0.0001	**0.0025**	0.0001
P. grandisquamis	0.0001	0.0001	0.0001	1	0.0001	0.0001	0.0001
P. opercularis	0.0001	0.0001	0.0001	0.0001	1	0.0001	0.0001
P. panamensis	0.0001	**0.0113**	**0.0025**	0.0001	0.0001	1	0.0001
S. peruviana	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	1

Bold numbers correspond to species without significant differences (Bonferroni=0.0024)

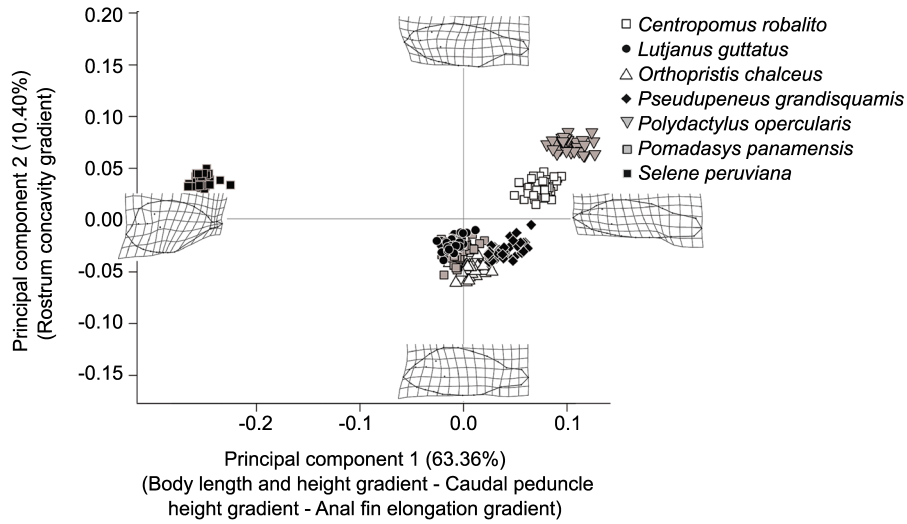


Fig. 4 PCA of morphometric information with the maximum positive and negative relative warps of each of two component axes (PC I= 63.36 %, PC II=10.40 %) axis of shape variation

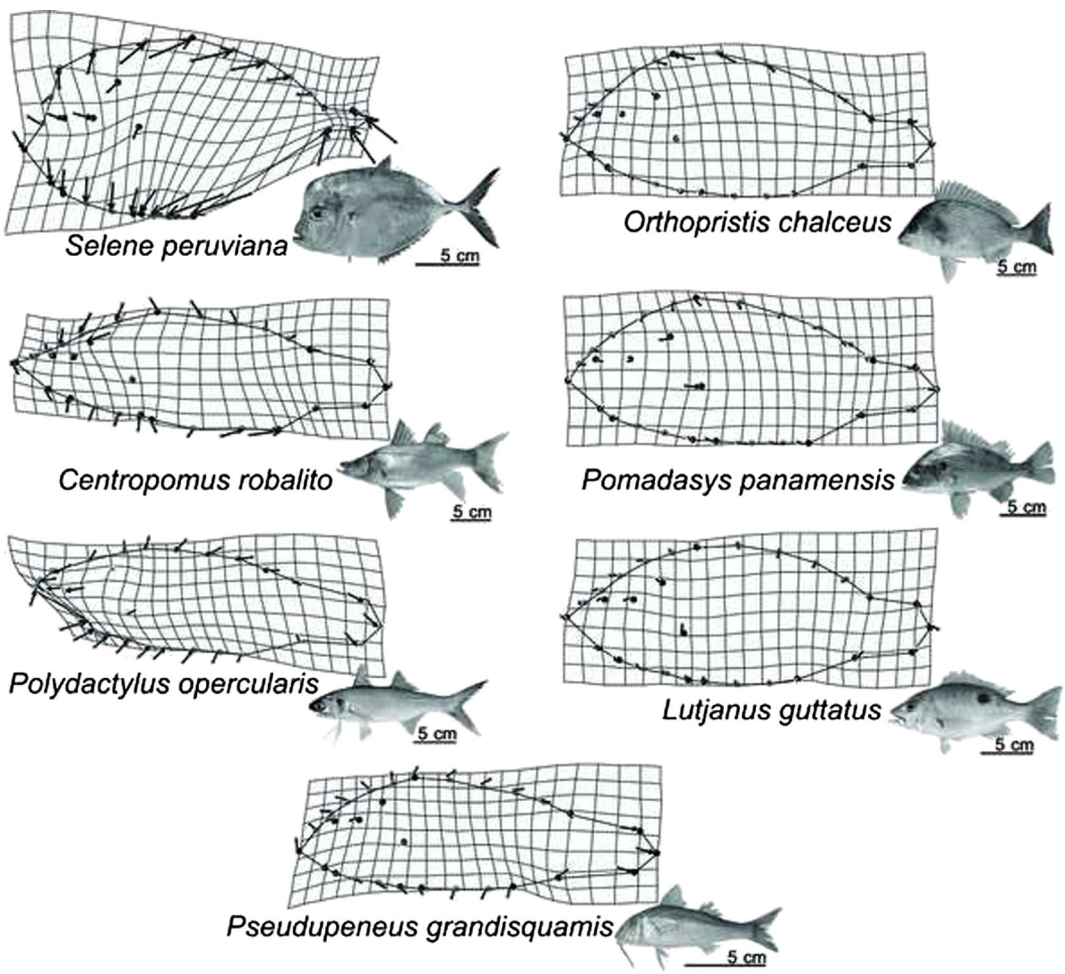


Fig. 5 Thin plate splines for each labeled species

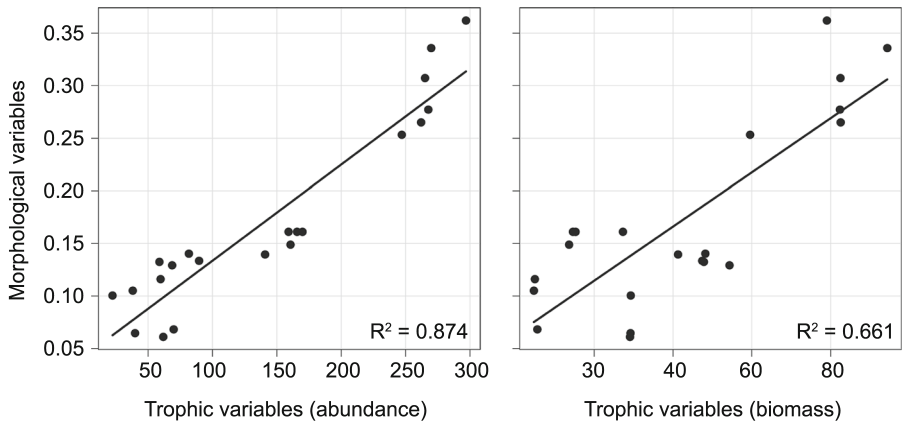


Fig. 6 Linear regressions between morphologic and trophic variables (left: abundance, right: biomass) for the seven demersal species analyzed. The variables correspond to the Euclidean distances between each pair of species

some species exhibited trophic variation that was greatly reduced (e.g., *P. panamensis* and *P. grandisquamis*), implying their diet was relatively specialized.

Discussion

As a result of their evolutionary history and to access to a greater variety of ecological niches, teleosts have evolved complex combinations of structures for carrying out processes of feeding, locomotion, respiration and reproduction, producing a high diversity of forms involving varied life histories (Motta et al. 1995a, b; Castro and Huber 2007). Thus, these organisms can be considered as model systems to discern the relationship between form and ecological function. Further, the body shape of each species allows us to infer aspects of their locomotion, thereby elucidating the extent and manner

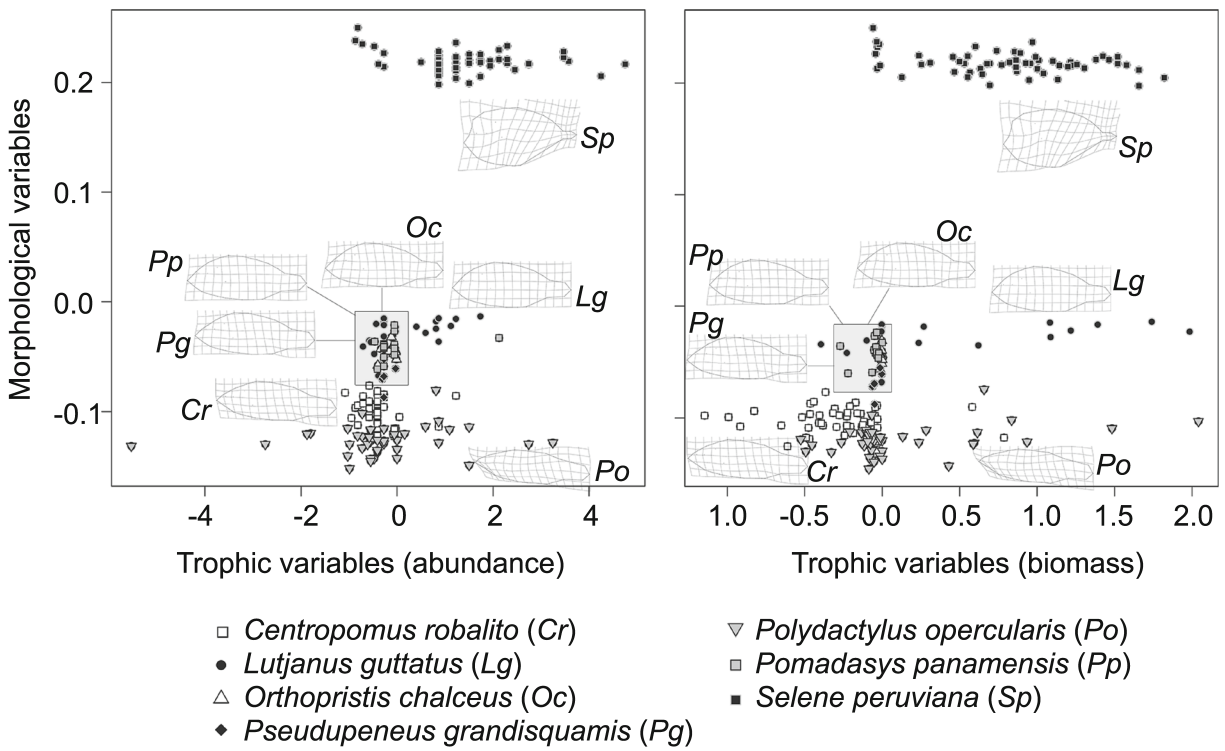


Fig. 7 Partial least squares analysis that shows the relation between morphologic and trophic variables [determined by abundance (left panel) and biomass (right panel) of preys]

in which each species exploits the available prey resources in the environment (Alexander 1978; Antonucci et al. 2009; Oliveira et al. 2010). During feeding behavior, predators often respond in such a way that implies they assume their prey will try to escape; thus the predators' objective is to minimize the escape possibilities of the preys, before they can maneuver or reach a hiding place (Webb 1984).

In this study we assessed patterns of trophic ecology and morphology in seven teleost species from the continental shelf in the Mexican Pacific. Though all species examined inhabit the same ecological zone (soft bottoms) and share the same prey base, trophic analyses revealed that many species differed significantly in their diets both in terms of abundance and biomass. Thus, the trophic analyses suggest that these species have diversified in their dietary niches, and have thus minimized competitive interactions through both resource specialization and temporal partitioning of prey acquisition (see supplementary material 1, temporal partitioning of resources). In particular, we found that species differed in the relative volume and abundance of different types of prey, notably crustaceans and teleosts, where some species (e.g., *S. peruviana*) utilized teleosts in greater frequency, while the diets of other species (e.g., *L. guttatus*) contained a higher proportion of crustaceans. These trophic differences also suggest that some bottom-dwelling fishes are more capable of obtaining distinct types of prey due to their structural or anatomical adaptations; a hypothesis supported by our morphological and ecomorphological findings.

In terms of morphology, we identified significant differences in body shape between nearly all species. These analyses revealed that *S. peruviana* was the most extreme species in terms of body form, displaying characteristics associated with both pelagic and benthic environments. For instance, *S. peruviana* exhibits a narrow caudal peduncle, a lunate caudal fin, and a high width-height aspect ratio, all of which are anatomical specializations allowing precise locomotion in pelagic environments, and extreme control of the angle of attack (Webb 1984). On the other hand, *S. peruviana* also displays a relatively short body, pectoral fins that insert in the middle of the body, symmetrical dorsal and anal fins that extend caudally, and a deep and laterally compressed body. These anatomical characteristics provide greater maneuverability to efficiently exploit resources associated with the benthic habitats (Webb 1984). This unique combination of anatomical characteristics suggests that *S. peruviana* can successfully utilize both habitats; a prediction supported by previous observations (Smith-Vaniz 1995). This combination of traits may also explain why *S. peruviana* is distinct from the remaining species in its body form, and why its trophic niche contains significant proportions of both benthic and pelagic prey.

By contrast, the remaining species display much greater similarity in morphology to one another when compared to *S. peruviana*. Here, these species have a relatively wider caudal peduncle and a more streamlined body shape that can maximize thrust and enables propulsion movements of high amplitude, allowing predators to capture evasive prey that requires a maximum level of acceleration (Webb 1984). However, whereas the trophic ecology of many of these species overlapped considerably, nearly all species could be distinguished because of their body shape.

Most notably, ecomorphological analyses revealed a significant association between trophic ecology and morphology for these species, and this pattern was identified both among species as well as at the individual level. These analyses revealed a pattern where fish displaying more pelagic characteristics in their body shape contained a greater volume and proportion of teleosts in their diet, while fish displaying a more benthic morphology with streamlined body and deeper caudal region preyed more heavily on crustaceans. These anatomical differences reflect functional differences in terms of prey capture, and correspond closely to the common prey identified in the respective diets of these species. Specifically, the escape strategies of teleost prey are characterized by forming schools, so predators need to develop a high swimming capability for relatively long periods. These are the locomotory characteristics exhibited by *S. peruviana,* which has a high proportion of teleosts in its diet. Interestingly, this species also shows an elongate anal fin, which together with the dorsal fin can generate nearly as much total force as the tail fin (Tytell 2006; Lauder and Madden 2007), as well as they provide balance when they fish needs maneuverability (Standen and Lauder 2007).

By contrast, crustaceans such as shrimp can only exhibit small bursts of fast escape behavior, and instead seek refuge sites in caves or in the substrate (soft bottoms). As such, their predators require morphological characteristics that allow them to perform fast accelerations for short periods, and display a more benthic morphology as represented by the other six fish species.

However, attack speed is not necessarily correlated with successful prey capture in these taxa, and other aspects should be taken into account. Specifically, the prey's reaction distance has shown to increase as the speed and the depth of the body profile of the predator increases (Dill 1974). Our six species displaying benthic morphology showed a low body profile, which contributes to their high prey capture rate, because this characteristic induces very short reaction distances in their prey (Webb 1984; Domenici 2010a, b). On the other hand, a rapid approach by the predator may trigger an early response in the prey, allowing it to escape; so the predators' fast-start performance is often sub-maximal (Webb 1984). Similarly, prey speed seems to be also sub-maximal when the predators attack is not followed by chases (Webb 1986); enhancing the species with benthic morphology, successfully capture their prey. Thus, whether observed at the individual or species level, our ecomorphological analyses reveal a strong association between foraging and body shape for these species.

Our results show that differentiation in trophic ecology among these species corresponds to substantial variation in body morphology. This relationship has been found previously for fishes in freshwater systems, like the stickelback *Gasterosteus aculeatus*, where interpopulation variability in the trophic morphology has been found to be a response to trophic resource differences between lakes (Lavin and McPhail 1985). Similarly, Gibson and Ezzi (1987) reported a positive correlation between mouth size (width and length) and prey length in demersal fishes. Rüber and Adams (2001) also reported an ecomorphological association in cichlids, where deep body shapes with ventrally oriented mouth (*Eretmodus cyanostictus*) were correlated with scraping feeding abilities. In contrast, a more fusiform body with an elongated head with a pointed snout and a shallowing in the head peduncle (*Tanganicodus irsacae*) were related with a faster maneuvering allowing the capture of mobile prey by picking. Likewise, Kassam et al. (2003) found the most pronounced variation in the head region of cichlids, implying that morphology has been adapted to different feeding strategies (zooplankton, benthophagous and limnetic feeders) among coexisting species.

Contrary to our study, a previous work on marine demersal fishes did not find any relationship between fishes morphology and feeding habits (Labropoulou and Markakis 1998), suggesting that evolutionary history and constructional constraints imposed by phylogeny, had more influence on morphology than the patterns of trophic organization within the fish assemblages examined. Although these authors analyzed morphological and meristic traits associated to feeding activities (ex. mouth width and height, intestine length, gill arch length, number of gill rakers, among others), those traits could be more related to physiological processes. Thus, they may be more related to evolutionary history than the traits that we analyzed which are more related to locomotion and maneuverability capabilities. Therefore, morphological traits related to locomotion and maneuverability might better explain the trophic variability of a species on a given place and time, along their ontogenetic history.

Webb's discussion of pelagic and benthic morphologies (Webb 1984, 1986) is one of the most classic views of the functional significance of morphological variation among fish species. However, several recent works have shown that this morphological gradient has influenced the functional abilities of individuals and thus their adaptive value for each species. For example, the responses to environmental characteristics (DeWitt and Scheiner 2004). Among some, phenotypic plasticity due to feeding habits seems to vary depending on the predator's presence (Brönmark and Miner 1992; Stabel and Lwin 1997), type of food (Day and McPhail 1996; Ruehl and Dewitt 2007) and environmental conditions (Parsons and Robinson 2006). Although our work analyzed a group of fish species in the soft bottom environment, we recommend the analysis of the phenotypic plasticity of each species along different environmental gradients.

In conclusion, our study reveals that the seven fish species analyzed here are well suited for the exploitation of soft bottoms habitats, and display both a partitioning of the trophic niche as well as different morphologies. The benthopelagic morphology is shown by *S. peruviana* whose shape enables to develop high swimming abilities for long periods, while chasing schools of teleosts. The other six species with benthic morphology are highly adapted to perform fast starts in short periods, as well as a low body profile which enables a 'stealth' approach posture to the prey without being noticed. As the ecomorphological relationships of several species of fresh water systems have been previously studied (Winemiller 1991a, b; Norton et al. 1995; Cochran-Biederman and Winemiller 2010), little is known about bottom-dwellers. Our study thus adds to this knowledge by demonstrating that the same types of

ecomorphological relationships found in freshwater systems also occurs in the soft bottoms habitats of the marine ecosystem.

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