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Morphometric Analysis on Shape Transition during Growth of the Red Snapper (*Lutjanus campechanus*, Poey, 1860)

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Abstract

The red snapper *Lutjanus campechanus* (Poey, 1860) has a high commercial value that sustains an important fishery in Mexico. In this study, the patterns in morphological variations from early juvenile to adult stages were assessed by geometric methods (GM) in 194 organisms. Changes in shape were more evident and rapid in the early juvenile stage and decreased during adulthood. The principal components analysis of shape (Relative Warp Analysis, or RWA) identified size and body depth as the main sources of variance associated to both juvenile and adult organisms. The outline of the head and the tail showed the most noticeable differences following the ontogenic pathway visualized by thin-plate splines indicating that the ontogenetic pathway of the upper half and the lower half of the dorsal head profile (DHP) are in relatively opposite directions than those from the tail that bends ventrally. The Two-Block Partial Least Square analysis (2B-PLS) and their CR coefficients showed that the two modules had a moderate linear trend ($p = 0.001$). Although the blocks have morphological changes at different rates, there is a moderate synchrony in growth by modules. This study is the first to report the use of geometrical morphometry in *L. campechanus* in Mexico.

Keywords

Lutjanus campechanus, Ontogeny, Shape, Integration, 2B-PLS, CR Coefficient

1. Introduction

During life, fishes respond to predictable and unpredictable environmental disturbances; in juveniles the main motto is growth and survival and in adulthood mating and perpetuation of the species is primordial [1]. Pelagic larvaes settle on benthic habitats and this process optimizes their performance in essential activities like swimming, evading predators, feeding skills and defending territories, also involving changes converging with the gradual modification of their body shape [2]. In this sense, it is important to evaluate the morphological variations observed during growth and also to know which characteristics remain from larvae into adulthood [3].

The differences in size of a given organism are commonly associated with variation in its shape [4], where many traits are highly correlated [5]. The effect of size on fish biometrics has been a topic of discussion in traditional morphometrics (TM) and geometric morphometrics (GM). In TM, correction methods are used to eliminate the effect of size defining only the variables that can describe only the shape of the object, but this strategy is questionable due to the variability of results obtained [6]. In contrast, GM addresses comparisons between shapes during development focusing in the analyses of the Cartesian coordinates of the anatomical points that are of biological interest [4], and bases its methodology in the use of landmark coordinates (LM) that gather datasets of two or three coordinates. This method provides a robust tool to quantify the simple shape of a given geometric object without considering the effects of size, rotation, and translation, but conserving in this way information on the relative spatial locations of the data that allows the differentiation either at individual or at group level [7]. The variation in the allometric growth is not influenced by the analysis because there are no restrictions in the variability of changes in shape with these techniques [8]. GM analyses are very useful for the study of organisms that have completed morphogenesis, and that are at different growth stages, where the homologous characters are identified throughout all the life stages [2] [9]. The benefit of a quantitative description is the accuracy that provides the ability to recognize intermediate shapes, to judge degrees of proximity or similarity to other shapes and to extrapolate or predict possible shape extremes [9] [10].

Allometry provides information on growth regularities, evolution, and size changes required in shape for maintaining organism functionality in specific environments [11]. This variation could be generated by different biological phenomena including static allometry (intraspecific allometry) which reflects the individual variations within a single population and group of age; ontogenetic allometry that occurs due to development processes; and evolutionary allometry that reflects the covariation of different phylogenetic traits between taxa [12].

In organisms with modular organization, there are other levels of allometry which reflect morphological flexibility in response to the environment [5]. The phenotypic evolution studied trait by trait suggests that the body is composed of integrated units that are considered modular parts and are integrated into characters that are functionally related to evolutionary transformation units [13]. The modules consist of structural elements—or parts—that are to some extent morphologically and evolutionarily different or that develop over contrasting times [14]. They maintain an internal relationship through multiple connections and interactions but remain relatively independent from each other in a way that the boundaries of each module can be recognizable [14] [15]. This pattern of strong internal connections and weaker external links is known as modularity that influences the patterns of morphological and evolutionary development.

In this sense, if the aim is to identify whether two or more structures are integrated through the ontogenic process, Partial Least Square (PLS) analysis provides an alternative to multivariate regression [4] [16]. This procedure is inferred from data obtained by the covariance analysis of multiple traits that have different degrees of emphasis due to the covariance strength, which is related to the variation between the dimensions of the morpho-space. The integration is stronger if all the variations are concentrated in one dimension, indicating a perfect correlation between all the measurements [15]; on the contrary, a fragile integration is when the connections between the different modules are scanty [16]. This process can be evaluated using two-block Partial Least Square analysis (2B-PLS), which consists of a set of external relationships (X and Y as individual blocks) with an internal connection (linking the two blocks) [17]. The above are used in GM where one or both variables correspond to shapes, such as landmark coordinates of Procrustes aligned specimens or partial warp scores [18].

The red snapper *Lutjanus campechanus* (Poey, 1860) inhabits the continental platform in the Gulf of Mexico, from the Yucatan Peninsula and the southwestern of the Gulf of Mexico up to Key West in the Atlantic Coast [19]. Juvenile stages grow in shallow waters characterized by muddy and sandy landscapes, while adults live in rocky bottoms and reefs that provide shelter and food with a range of distribution in the water column from 10 m to 190 m depth [2] [3]. Maximum reported sizes range from 82 to 88 cm (in total length) and reproduction occurs over a period of nine months, with peaks in June to August, with a proportion of sexes (F:M) of 1.06:1.0 and size at maturity reported of 24.2 cm in males and 28.3 cm in females (total length) [20] [21]. In Mexico this species is under intense commercial and recreational fishing without effective regulation, despite being included in the IUCN Red List of threatened species with the category of Vulnerable (VU) [22].

The aim of this study was to evaluate the static ontogenetic growth of *L. campechanus* from early juvenile to adult stages using GM traits to establish morphological trends of the changes in trajectory and direction associated to shape occurring in these developmental stages to establish its integrative and/or modular nature, and to infer the ecological implications in each stage.

2. Material and Methods

2.1. Study Area

The Campeche Bank is located within the ecoregion of the Southern Gulf of Mexico and extends between 19˚23'N and 89˚93'W in the southern Gulf of Mexico. This region is the natural habitat of *L. campechanus* (Poey, 1860), being characterized by bottoms that have a bed suitable for the development of reef and rocky benthic communities, which are appropriate for the settlement of this species [23] (**Figure 1**).

2.2. Sample Collection

Between January and February of 2015 (northerly winds season), a total of 194 specimens with sizes ranging from 3 to 30 cm in standard length (SL) were purchased from commercial fleet that holds commercial permits and follows the guidelines established by the Mexican Regulations Fisheries NOM-002-PESC-2013 and by the National Fisheries Chart (DOF 15/03/04) and (SNFA/034/12). These permits are issued every two years by SAGARPA (Secretaria de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación) (https://www.inapesca.gob.mx/), based on their commercial catch. Juvenile red snappers were collected by shrimp trawls, whereas adults (larger than 20 cm SL) were collected with hand lines; organisms were purchased dead, maintained horizontally and kept in containers with ice until their arrival to the laboratory, where they were maintained at -20˚C for the subsequent analyses.

2.3. Data Acquisition and Analysis

The specimens were separated into 6 size classes: CL0: 3.0 - 4.9 cm (20 organisms), CL1: 5.0 - 9.9 cm (35 organisms), CL2: 10.0 - 14.9 cm (31 organisms) CL3: 15.0 - 19.9 cm (32 organisms), CL4: 20.0 - 24.9 cm (40 organisms) and CL5: 25.0 - 29.9 cm (35 organisms). The CL0, CL1, and CL2 classes corresponded to pre-recruits and early juveniles, while CL3, CL4, and CL5 classes included juveniles larger than 15 cm, pre-adults and adults (individuals that had reached the size of their first sexual maturity) [21].

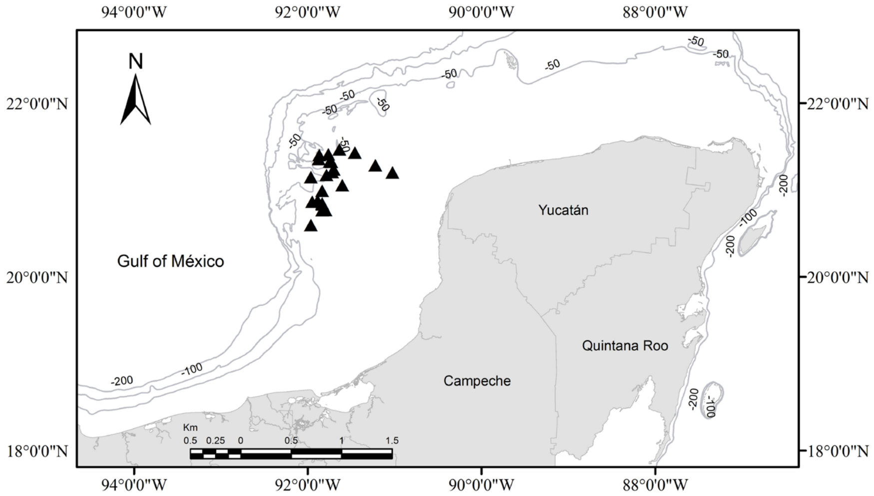
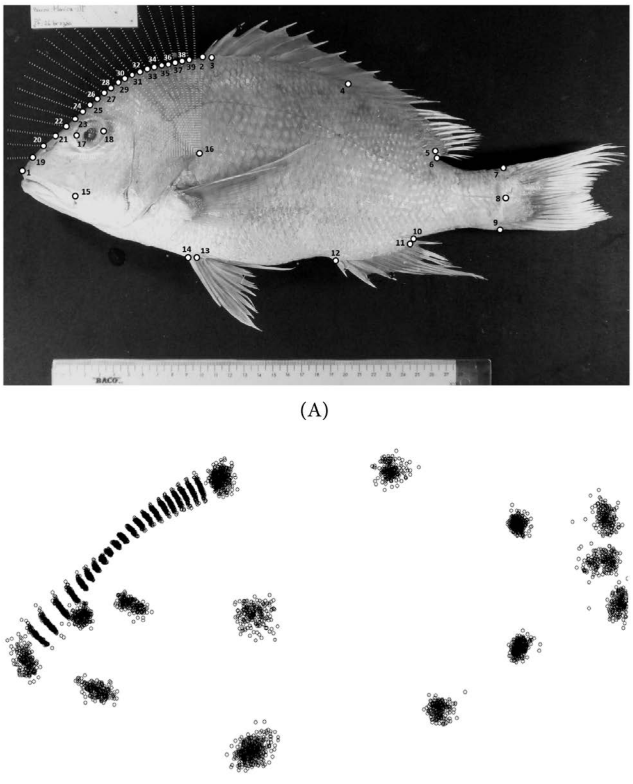


Figure 1. Sampling sites in the Campeche Bank, all locations are localized in the quadrant formed by 21˚32'34.62"N - 92˚03'48.22"W and 20˚30'29.52"N - 90˚56'31.55"W coordinates.

Each specimen was photographed from its left side using a digital Olympus camera, with a resolution of 12.4 megapixels and macro option. The tripod was 50 cm distant from the baseboard and the camera was attached to a sliding arm to control the distance. The baseboard was covered with black plastic (ethylene vinyl acetate), to avoid the light reflexion and the presence of shadows.

The morphometric analyses were carried out based on a series of landmarks (LM) and sliding reference points (*i.e.* semi-landmarks: SLM), defined as the whole fish and the dorsal head profile (DHP) respectively. The selection of the appropriate LM was carried out based on the typology proposed by Bookstein [24], these correspond to types 1 and 2 and the SML to type 3. The final points consisted of 18 homologous points arranged along the fish's body (points 1 - 18), and 21 SML (points 19 - 39) along the curvature of the DHP (**Figure 2(A)** & **Figure 2(B)**).

The program MakeFan6 was used to position the semi-landmarks SML equidistantly along the DHP [25]. Homologous landmark 1, 2 and three were used supporting points to draw a fan on the cranial region; these corresponded to the most distal point of the upper jaw, from the first spine of the dorsal fin up to the most distal point of the operculum. TPS files were generated using the software tpsUtil 1.58 [26]. Landmarks and SML were digitalized using the program tpsDig 2.16 [27]. Analysis of the LM data allowed the quantification of the changes in


(A)

(B)

Figure 2. (A) The configuration of landmarks (LM: 1 - 18) and semilandmarks (SLM: marks 19 - 39); (B) Procrustes superimposition of 194 specimens.

shape and direction throughout the development [8], for this, a non-parametric analysis and a morphometric-type exploratory analysis was performed.

The LM configurations were superimposed using the Generalized Procrustes Analysis (GPA) [28] [29]. The centroid and the effects due to the location, scale, and orientation of each of them were determined and removed using the Procrustes superimposition method of generalized least squares (GLS) [14]. These methods were used to record the LM configurations in a coordinate system that then is used as geometric variables [30]. The remaining differences in their location within the coordinate system were attributed to variation in shape. All data acquired were used as input data in the multivariate analysis.

The spline relaxation technique was also used to know if there was any change over the bowing on DHP at the same time of the development of the body: this procedure expands on the standard Procrustes superimposition method (GLS). The SML are slid along the curve of the profile until the positions of the corresponding points match as a reference configuration as closely as possible [31]. This analysis is called Relative Warp Analysis (RWA), and minimum Procrustes distance criterion was used. The Bookstein algorithm [24] was used, and then the points were slid along the tangent to the curve with 40 iterations. An alpha = 1 was used because the allometric effects tend to be large-scale [32]. After relaxation, the SLM were treated as if they were homologous reference points in the multivariate analysis [4].

After sliding, the Procrustes superimposition was recalculated to eliminate the information based on the original coordinates. This procedure was performed to standardize each specimen to a unit centroid size (CS: is a measure of geometric scale, defined as the square root of the sum of the squared distances of each reference point) [33]. The coordinates of all the aligned specimens were compared using the TPS function as a deformation method. In this way, the partial warps and their principal components or relative warps were calculated. The CS was obtained from this analysis, which represents a dispersion measure of LM around of the centroid. Further, a Principal Components Analysis (PCA) was performed on the weight matrix obtained from the RWA to examine the major trends of body shape variation.

Deformation grids were also obtained using a thin-plate spline analysis. This grid graphically described the variation between specimens by using the morphology of all the specimens to obtain an average shape where the position of the landmarks was compared, and the differences were represented as a deformed grid. Then changes in DHP shape were visualized to observe possible modifications in its curvature during fish development. These deformations were exaggerated three times to have a better perception of the morphological differences between classes. These analyses were performed in the tpsSpline 1.20 [34] and the tpsRelw 1.49 programs [35].

To evaluate the influence of size on shape, we performed a correlation analysis using the standard length against the CS (untransformed). The correlation value was $r^2 = 0.999$ ($p < 0.001$), and the centroid was used as a proxy in all the subsequent analyses.

The differences between classes as a possible consequence of the change in the coordinates set during fish growth were evaluated by a one-way PERMANCOVA (999 permutations) performed over a Euclidean distance matrix (after log-transformation of the CS data). The partial warp scores generated for the Relative Warp Analysis were considered as variables, the logarithm of the centroid (LogCS) and SL were included as covariates and the classes as fixed factor. The CS is often used as a covariate in the morphometric analysis to consider the possible allometric effect of a size that is not explained by the scaling function of Procrustes superimposition [36]. This analysis was performed in the R package.

2.4. Modularity and Integration Analysis

The morphological integration between different regions of the body was evaluated using the "two-block Partial Least Square" (2B-PLS) analysis to establish the covariation of shape along the body among various modules. This procedure was performed using the tpsPLS program [37] creating pairs of variables, which are linear combinations of the original data of each block [18]. This test was also used to determine the combination of variables, in the two sets, that explained the highest covariation between them. The 2B-PLS analyses the variables of both modules symmetrically [*i.e.* it is not assumed that one set causes the other, that they are linearly related to one another, reflecting the responses of the underlying (unobserved) or latent variables] [4]. The correlation coefficient "r" can be used as a measure of integration between the sets [15] [38]. The statistical validation for the 2B-PLS analyses was performed through a bootstrap test of 9999 permutations to determine whether the unique values produced were consistent with the null hypothesis of no significant covariance in the patterns between sets.

Modularity was evaluated using the CR coefficient (the covariance ratio) to verify the consistency of the results of the analysis of integration achieved by the singular warps analysis [39]. The CR coefficient is not affected by the sample size, or the number of variables (LM). Before the analyses, data were aligned using the Generalized Procrustes Analysis (GPA).Both indices range between 0 to 1 value, where 0 indicates the independence between modules and, therefore, the presence of modularity; and 1 implies a process of integrated development. 999 iterations were used to evaluate the level of significance during the procedure of permutations. Both analyses were performed in the R package Geomorph [40].

During growth, fish evolve hydrodynamic skills to guarantee survival at every stage of their life. They swim either using the body and the caudal fin, or a combination of the dorsal-anal fins and the pelvic-pectoral fins [41]. The body shape grows from a slender shape in the larval stage into a streamlined adult to provide very little resistance to the flow of water and to optimize its performance [42]. Based on these premises; the body of *L. campechanus* were partitioned in three modules: head (HD), trunk (TR), and tail (TL) to assess their modularity by growth and by class (**Table 1**). Each block landmarks were selected based on the same homology criteria; all points should be observed in the distinct stages of development to describe the transition from juveniles to reproductive adults.

3. Results

The PERMANCOVA analyses exhibited significant differences between classes ($p < 0.001$) showing that the LogCS covariate has a significant relationship with the morphometric coordinates ($p < 0.001$). Although, the Classes-LogCS interaction was not significant (**Table 2**). The RWA values are described in **Table 3**. The first two elements provided the greatest information (95.93%) on the morpho-space composition and reflected a deep contrast between the shapes of each class.

The LogCS had highly correlation with the standard length ($r = 0.969$, $p < 0.01$) (**Figure 3(A)** & **Figure 3(B)**), (*i.e.* the shape is related to size, although the relationship is not purely linear). Conceptually, the CS is independent of shape, and it is only correlated when growth is allometric. For the variables LogCS and SL vs. RW1, the correlations were weak (**Figure 3(B)** & **Figure 3(C)**). The correlations between RW2 and the variables Log CS and SL showed a moderate significant negative correlation with a large scatter of points. This could be

Table 1. Modules with specific landmarks and their individual description used in the Two-block Partial Least Square Analysis (DPH: dorsal head profile, LM: landmark).

Module	LM	Location of homologous reference points
	1	Most distal point of the upper jaw
	2	First spine of the dorsal fin
Head	14	First spine of the pelvic fin
	15	Commissureofmouth
	17 - 18	Eye
	16	Most distal point of operculum
	19 - 39	Semi-landmarks. DPH between LM 1 and 2
	3	Second spine of the dorsal fin
Trunk	4	Last spine of the dorsal fin
	5	Second last ray of the dorsal fin
	11	Second last ray of the anal fin
	12	First spine of the anal fin
	13	Second spine of the pelvic fin
	6	Last ray of the dorsal fin
Tail	7	Beginning of the caudal fin (dorsal view)
	9	Beginning of the caudal fin (ventral view)
	10	Last ray of anal fin
	8	Final lateral line

Table 2. PERMANCOVA used over classes to categorize the developmental stages in red snapper (*L. campechanus*) (Poey, 1860). LogCS and SL were used as covariates. Significant results are shown in bold ($p < 0.001$).

	Df	SS	MS	*F*	P
Classes	1	9.0086E^{25}	9.0086E^{25}	29.7916	0.001
LogCS	10	1.8070E^{26}	1.8070E^{26}	5.9757	0.001
SL	1	2.9029E^{24}	2.9029E^{24}	0.9600	0.394
Classes: LogCS	4	9.7753E^{24}	2.4438E^{24}	0.8082	0.616
Classes: SL	1	1.1822E^{24}	1.1822E^{24}	0.3909	0.777
Residuals	176	5.3220E^{26}	3.0239E^{24}		
Total	193	8.1684E^{26}			

Table 3. Principal component analysis (Relative warp analysis) (SA: singular axe; SV: unique value).

SA	SV	% Explainedvariance	% Cumulativevariance
1	1.58E24	66.25	66.25
2	7.09E23	29.68	95.95
3	8.34E22	3.49	99.42

because the RW2 axis expresses the contrast between the length and width of each specimen (**Figure 3(D)-(F)**). Although between RW1 and RW2 no correlation was observed (**Figure 3(F)**).

The distribution of the specimen scores along the first two components is shown in **Figure 4(A)**. The Relative Warp 1 explained 66.25% of the variance; the primary variables of greatest value along this axis are in the DHP and corresponded to the SLM that described the change in the form as the body size increased showing an enhanced enlargement of the caudal peduncle. RW2 explained 29.68% of the variance, this axis described the augmentation of the height of the organisms according to their growth (LM 2 y 14); similarly, the variables of greatest value corresponded to the DHP (SLM plus the consistent element).

The results of the deformation grid for all the organisms showed that the regions of greatest variation were in the DHP and in the caudal region (**Figure 4(A)** & **Figure 4(B)**). The projection of the displacement path of the LM on the upper half and the lower half of the DHP are in opposite directions and the LM of the caudal region are projected in the ventral direction, demonstrated by differences in the PC1 scores.

From the visual inspection of the deformation grids by class (**Figure 4(A)**), the main changes were observed in the head, and tail and they are more evident between classes 0, 1 and 2 *vs.* class 5, corresponding to recruits and early juveniles. The first two categories were characterized by large eyes close to the mouth that migrated to opposite positions in the largest class, while the profile becomes

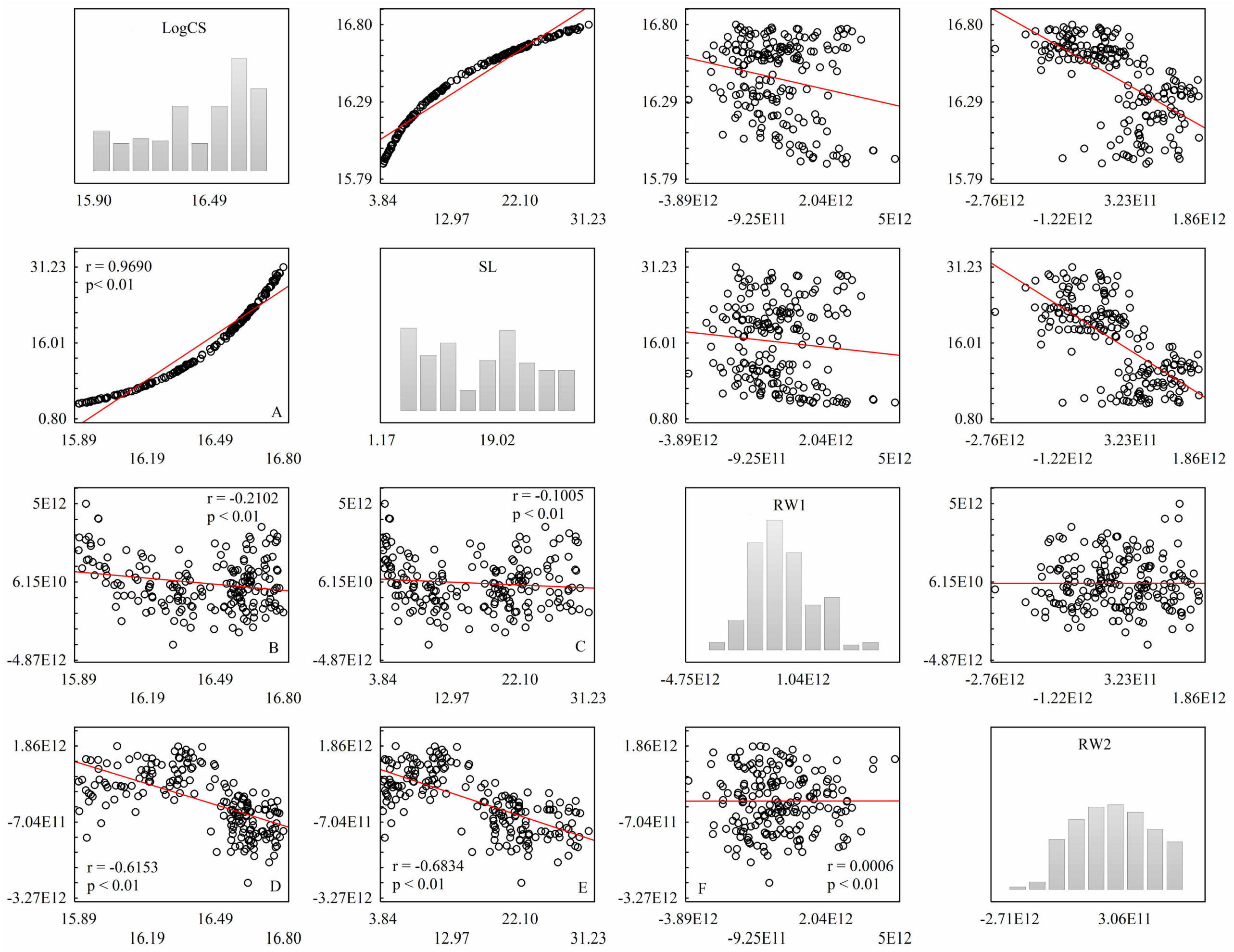


Figure 3. Matrix plot of correlations between the centroid logarithm (LogCS), standard length (SL) and relative warp axe (RW1 y RW2 scores). Regression values (r) and p-values are reported for each graphic. The frequency histogram represents the distribution of each variable.

more convex (**Figure 4(A)**). The gradual change in the direction of the mouth suggested an increase in the height of the rostrum. The trunk showed an increase almost proportional to the size of the head. The relationship between the trunk and tail (**Table 5**; $r = 0.621$; $p < 0.001$) is moderate, in the first classes the caudal peduncle is short and robust, getting longer and thinner towards the larger sizes. Visually constant changes are observed in the head and the tail, which seems more independent in comparison with changes compared to the other two modules, whereas the head and trunk are slightly more integrated regarding morphologic variations (**Figure 4(A)**).

Modularity and Morphological Integration: Shape analysis between blocks

The covariance between the pairs of modules analyzed was significant in all cases; the first singular value explained more than 90% of the total covariance for the HD-TL and TR-TL modules, and almost 75% for the HD-TR module (*i.e.* only one dimension shows significant covariance) (**Table 4**).

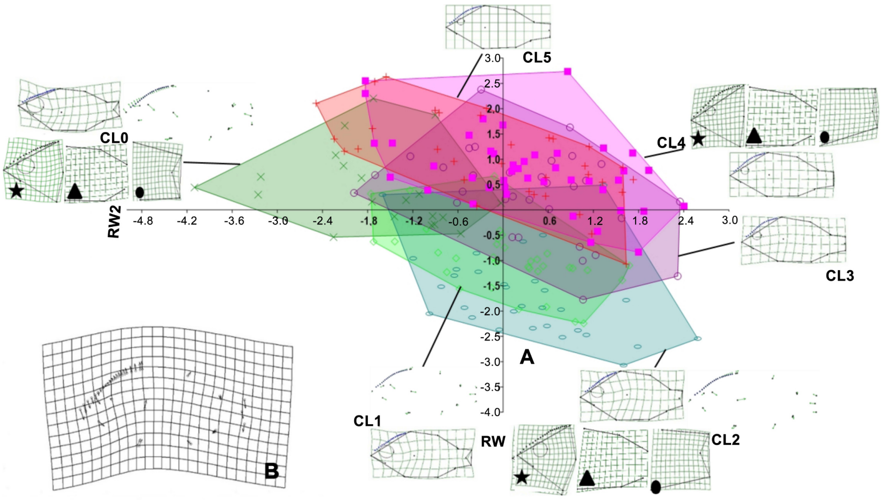


Figure 4. Consensus outline: (A) Relative Warp Analysis considering all landmarks (LM = 39) and all the samples (194 organisms). (B) Movement path of the landmarks (all specimens). CL0: Class 0 (**X**, 3 - 4.9 cm, recruitments), CL1: Class 1 (◇, 5 - 9.9 cm, early juvenile), CL2: Class 2 (○, 10 - 14.9 cm, juvenile), CL3: Class 3 (O, 15 - 19.9 cm, juveniles > 15 cm), CL4: Class 4 (■, 20 - 24.9 cm, pre-adults), CL5: Class 5 (**+**, 25 - 30 cm, adult stage). HD: Head★, TR: Trunk, ▲, TL: Tail ●.

Table 4. Total covariance explained by the first two singular axes and the covariance ratio for each module pair analyzed (CR coefficient).

Module	Two block PLS				CR coefficient	p-value
	SA	Covariance	Percentage (%)	% Cumulative		
HD-TR	1	3.572988^{E-004}	75.64	75.64**	1.5657	0.572
	2	1.661885^{E-004}	16.36	92.00		
HD-TL	1	1.163037^{E-003}	94.22	94.22*	1.0761	0.454
	2	2.310082^{E-004}	3.72	97.94		
TR-TL	1	8.460028^{E-004}	95.98	95.98*	1.114	0.618
	2	1.212076^{E-005}	1.97	97.95		

(*p < 0.001; **p < 0.05; n = 194). (SA: singular axes, HD: head, TR: trunk, TL: tail). *, **statistical significant differences.

The highest correlation values were found between the HD-TR (0.684) and the HD-TL (0.663) with high significance (Table 5; p = 0.001). The highest correlations were observed in dimension 1, and for the remaining dimensions the correlations were weak but significant. The values of correlations suggest that there is a moderate relationship between modules that increased slightly independent. The covariation between modules per class was almost equal for the two first axes in most of cases, although the cumulative percentage values for these axes only explain between 80% - 88% of the variance.

The CL0 class showed the greatest covariance values between the HD-TL modules (r = 0.706 on dimension 1 and r = 0.815 on dimension 2), but it was significant only for dimension 2 (p = 0.005); the correlations between the other pairs of blocks for this class was moderate but not significant (Table 6).

Table 5. Correlation analysis between the scores of the specimen's vectors along the singular axes of each pair of blocks by dimension (permutations: 9999; *p < 0.001, **p = 0.0001; HD: head, TR: trunk, TL: tail; n = 194).

Module	Dimension 1	Dimension 2
HD-TR	0.6836**	0.4621**
HD-TL	0.6628**	0.2836*
TR-TL	0.6210**	0.2479*

*, **statistical significant differences.

Table 6. Two-block Partial Least Square and the CR coefficient Analysis between module per class (p < 0.001; DIM = Dimention; CL0: Class 0, CL1: Class 1, CL2: Class 2, CL3: Class 3, CL4: Class 4, CL5: Class 5; HD: Head, TR: Trunk , TL: Tail).

Two block Partial Least Square						
Class	MD	DIM	r	p-value	CR coefficient	p-value
CL0	HD-TR	1	0.692915	0.233	1.0022	0.149
		2	0.670554	0.234		
CL0	HD-TL	1	0.705276	0.1945	1.045	0.212
		2	0.815714	0.0049*		
CL0	TR-TL	1	0.603293	0.577	1.1158	0.633
		2	0.583458	0.294		
	HD-TR-TL				1.0479	0.189
CL1	HD-TR	1	0.648690	0.0306*	1.0726	0.449
		2	0.674212	0.0047*		
CL1	HD-TL	1	0.638292	0.0283*	0.9447	0.019*
		2	0.502885	0.2481		
CL1	TR-TL	1	0.492600	0.435	1.1143	0.688
		2	0.607666	0.016*		
	HD-TR-TL				0.9871	0.05900*
CL2	HD-TR	1	0.457796	0.808	1.0473	0.334
		2	0.493198	0.429		
CL2	HD-TL	1	0.709059	0.003*	0.9286	0.00800
		2	0.503635	0.218		
CL2	TR-TL	1	0.440186	0.587	1.0933	0.399
		2	0.460770	0.216		
	HD-TR-TL				0.9984	0.047*
CL3	HD-TR	1	0.556855	0.156	1.0615	0.387
		2	0.606045	0.023		
CL3	HD-TL	1	0.553937	0.160	0.9888	0.031
		2	0.516882	0.053		
CL3	TR-TL	1	0.493622	0.339	1.0897	0.455

Continued

		2	0.457373	0.251		
	HD-TR-TL				0.9647	0.031*
CL4	HD-TR	1	0.768343	0.0001	1.06	0.428
		2	0.443860	0.151		
CL4	HD-TL	1	0.319136	0.981	1.0639	0.185
		2	0.316065	0.821		
CL4	TR-TL	1	0.569432	0.124	1.0441	0.393
		2	0.381886	0.491		
	HD-TR-TL				1.0454	0.083
CL5	HD-TR	1	0.523639	0.0789	1.0723	0.442
		2	0.535135	0.0418*		
CL5	HD-TL	1	0.486377	0.1834	1.0579	0.164
		2	0.350178	0.628		
CL5	TR-TL	1	0.541645	0.093	0.9859	0.252
		2	0.501468	0.084		
	HD-TR-TL				1.0252	0.041

*Statistical significant differences.

Class 1 exhibits a moderate significant correlation in HD-TR ($r = 0.649$ on dimension 1 and $r = 0.674$ on dimension 2; $p < 0.05$) and HD-TL blocks present a $r = 0.638$ ($p > 0.05$) in dimension 1; the blocks TR-TL show similar value but for dimension 2 ($r = 0.608$; $p > 0.05$). The pre-recruits and recruits of classes 0, 1 and 2 were characterized by oral structures that dominate in relation to the size of the head, in this block we found the most obvious sources of variation because the form of the head had a rising pattern from the oral opening and this marks tend to maximize the ability of the buccal opening. The structures of the mouth had morphological changes with growth related to eating habits and the way of obtaining prays from juveniles up to adulthood [43]. Another modification observed was in the eye area where the convex curvature of the eye increased from the longitudinal axis of the head.

Classes 2 and 3 showed similar *r*-values patterns in HD-TL blocks (dimension 1: $p < 0.05$) and HD-TR (dimension 2: $p < 0.05$). Class 4 revealed a moderate correlation with a strong statistically significant value ($r = 0.77$, $p = 0.0001$) in dimension 1and in the module HD-TR. Finally, Class 5 showed a weak to moderate correlation in HD-TR modules in dimension 2 ($r = 0.535$, $p < 0.05$).There was a change in the cauda; it started from short and broad in recruit stage and changed into a slender and large in juvenile stage (CL1, 2 and 3). Meanwhile, the TR module did not show changes throughout the different classes, although statistically significant values are presented in the CL3 and CL4 involving a slight asynchrony in its growth, probably to compensate changes in the opercular area.

The covariance pattern between blocks with all the specimens provided the highest resolution. All the patterns between sets for each class were characterized by more noticeable changes during early juvenile and juvenile stages and slower changes in stages that comprise the larger classes (**Figure 4(A)**). Despite this, the morphological changes in the blocks adjusted the relative positions of the landmarks as they increase in size remarking the high synchrony between the growth of the modules.

In the HD-TR covariance, the first two classes were probably associated to changes in the morpholpogy of the head and to a lesser extent to the displacement of the fins between both modules; whereas in the remaining classes, changes were only detected in the area of the nostrils and eyes because the shape of the head was more streamlined in the larger classes.

The results obtained with the CR coefficient, using the total number of copies by module (*i.e.*, $n = 194$), did not show the same trends of statistical significance as the 2B-PLS analysis; according to this coefficient, *L. campechanus* had a highly integrated development process but it was not statistically significant (**Table 4**).

When the three modules were analyzed at the same time by class (HD-TR-TL), the values of $CR = 0.9$ were statistically significant ($p < 0.05$) (**Table 6**). Although, with this analysis it was not possible to know which pair of modules contributed to this variation. The analysis of modules per pairs registered a slight independence between HD-TL, which is statistically significant for the classes 1, 2 and 3 ($p < 0.05$). This trend was similar to that obtained in the 2B-PLS.

In CL5 the value of CR of the three modules suggested the same trend, but this was not detected in the analysis of modules by pairs, although the 2B-PLS logged a statistically significant correlation between the HD-TR modules of classes 3, 4 and 5 indicating that there is a moderate independence between both modules in larger classes. In this case the first two dimensions provided more information about the composition of the morpho-espace and reflected certain contrasts between forms of every kind. Once again, probably due to the change in eating habits of juveniles and adults.

4. Discussion

The ecomorphology approach studies the interaction between morphological and ecological diversity, to explain the morphological variations in individuals that result in functional differences and development [44]. In fishes, there is a clear relationship between shape and function allowing morphology to reflect adaptation to habitat and feeding niche [45]. Fishes comprise one of the most taxonomically diverse taxa, and their morphology varies intra specifically and inter specifically conditioned by different development pathways and functions, which depend on different behavior and lifestyles within a wide variety of ecosystems. Although the hydrodynamics of marine environments impose severe restrictions on their design, the presence of thousands of species living in different habitats demonstrates the existence of a wide variety of shapes. In that sense, some species can be classified according to a functional category about their shape (rover-predator = fusiform, bottom fish = flatfish, deep-body fish = compressiform), and *L. campechanus* is categorized as compressiform associated to the structure of its habitat characterized by coral reefs [46].

Lutjanids, a group composed by125 species, are generalist predators that belong to the rover-predator category with a downward mouth [19]. Typical snappers have a heavy and fusiform body with a dorsal fin, a sturdy and tight caudal peduncle and a slightly forked fin, and during the adult stage they have a triangular head with a large protractile mouth at the apex of the triangle, with fins distributed uniformly along the body, providing stability and maneuverability for their carnivorous habits [46].

4.1. Shape Variation and Developmental Pattern

The outcomes of this study represented a quantitative assessment of the shape of *L. campechanus* that provide more information on their morphometrics analysis. The sliding semi land-marks technique was used to explain changes in homologous anatomical loci with emphasis on the processes that modify the DHP curve during growth as a way of explaining the streamlined swimming ability that they experience during the distinct stages of their cycle.

During growth, the juveniles must achieve a high survival rate, and this process requires compensatory allometric changes in size so that functional abilities can be maintained until fish reach adult size [43]. The increase in fish size influences dramatically the performance in certain fundamental aspects of the interaction between the individual and the environment. Without these changes, the ability of adults to perform certain tasks, such as swimming, may be affected unless the initial performance levels are high enough to absorb reductions in their size-related skills [47]. In *L. campechanus*, the RWA showed a continuous distribution of specimens along the two principal axes. Samples that were either very positive or very negative along RW2 have a strong influence on the allocation of the values of the evaluated traits and revealed contrasts in shape related to the length and depth of the body for the size classes. The negative values along both axes corresponded to smaller size classes (CL0, CL1, and CL2), whereas the positive values corresponded to classes with an SL that exceeded 15 cm. The specimens were equally distributed across the suggested size classes; hence the plot suggested that there was no clear size structuring in the populations from the catching site.

Lutjanidae family have both positive and negative allometric development [48] [49]. Mbaru *et al.* [48], Gómez *et al.* [50] and Manickchand-Heileman & Phillip [51] reported almost isometric growth in *L. bohar*, *L. vivanus*, and *L. purpureus* respectively. In its early larval stage, *L. campechanus* (Poey, 1860) has an allometric growth pattern, regarding to length of trunk on the standard length [52], allowing a faster development of the structures needed for feeding and locomotion [53] [54]. This could explain that the head showed great variations in the LM trajectories and tail of the smallest SL size classes (CL0, CL1, and CL2). In these groups, they are still growing, and their main functions are feeding and avoiding predation. The deformation grid of the thin plate analysis for each size class showed that the first three size classes had the most compelling changes in the head and caudal peduncle. It has been estimated that in larvae, the head can comprise up to 45% of the body length [55], a proportion that progressively decreases with growth.

All the variations experienced by *L. campechanus* (Poey, 1860) reflected a growth pattern like that found in the common carp [53]. These differential trends determine the size-shape relationship during ontogeny. When shape and size are linked by an allometric-type relationship, a change in size corresponds linearly to a change in shape [5]. An in theory, sizes larger than 50 cm SL of growth becomes almost isometric [56].

4.2. Hydrodynamics

Some fish use distinct parts of the body during swimming related activities like predator evasion, prey capture and navigation in structurally complex environments [57]. The hydrodynamics of the environment influence partially the shape of fishes; for example, macro carnivores have kept fusiform shapes enabling them to have less friction with the water to have a greater and faster displacement, and the environment that fishes face depends on the individual size, the speed at which it moves, and the physical properties of the water itself (viscosity and density) [58] [59]. During ontogeny, fishes regime changes on the environment, because they get bigger and faster, and the relationship between inertia and viscosity change as they develop, altering their swimming behavior [42] [58] [59], which will affect the ability to escape predators [60].

The types of forces acting on a moving fish differ according to the hydrodynamic regime. The Reynolds number is used as an index to identify the hydrodynamic regimes experienced by the fish: $Re = UL/v$, where U and L are the velocity and length of the fish and v are the kinematic viscosity of the water [61]. The regime of inertial forces dominates when $Re > 200$ (inertial regime), however, viscous forces prevail when $Re > 1$ (viscous regime) and are significant for larvae up to $Re = 30$. At $30 < Re < 200$ an intermediate zone is estimated, in which the balance between the two forces is gradually displaced from a viscous liquid to an inertial regime. Borazjani & Sotiropoulos [62] found that at low *Re* the larvae present greater fluctuations in swimming speed than adult fish; their results demonstrate that all fish swam more efficiently if they had a body shape or swimming style suitable to the speeds at which they swam. The fish swimming speed leads to rates of hydrodynamic forces that will influence the body shape and swimming style in subsequent stages favoring the balance between swimming bursts, needed for a rapid response to predation events during the youngest stage and the swimming sustained. These features are essential for activities such as foraging or searching for a mate in adult stages [36] [63] [64] [65].

In early stages (early juveniles and juveniles), *L. campechanus* (Poey, 1860) specimens had arge heads ending in a slightly pointed forehead and more sleek bodies when compared to adult shapes [21] [58]. This could explain the displacement paths observed in the thin plate analysis because the allometric growth influence over the variables of shape was detected with the PERMANCOVA analysis. In this case, the LogCS covariate explained a high percentage of variance on the effect of increase between classes. These changes in shape occurred mainly in the profile of the face and the structures of the head, in which the SLM undergo necessary changes in position on the anterior and dorsoventral axes of the body. The changes in shape reflected the transition from early juvenile to adult involving these regions, confirming the general findings reported in the RWA.

4.3. Modularity

Modularity is the partitioning of the integration into evolutionarily or developmentally independent blocks of traits. Sizes and shapes of the body (or their parts) vary in a coordinated manner as a whole functional group [15]. This process is measured by statistical associations between traits [66]. The structure of these associations reflects the processes that affect certain traits but not others. These are covariance-generating processes that influence the patterns of morphological integration [67] that can be modified by mutations, by development dynamics or by environmental processes.

The study of ontogenetic morphological development in fish was based on the study of allometric models of three different regions detected along the anterior caudal axis: head, trunk, and tail [2] [53] [68]. According to our results and the configuration proposed herein, *L. campechanus* (Poey, 1860) has a modular conformation during growth. The greatest covariance between the modules was explained by SA1, although there were no significant differences between values, there were slight differences in growth outlines along the anteroposterior axis. The correlation value between the head and the trunk indicated that these modules maintained a slight synchrony in the development process; a large head corresponding to a deep trunk and this proportion is clearer in larger sizes.

In this study, a certain pattern of morphological integration between the head and trunk was observed, although this relationship was not strictly linear. The development of the tail was modular and independent from the other blocks. The head and the tail developed before the trunk of the body, and increases in depth quite late in development, this because of a possible adaptation to reduce transporting costs [54].

Genetic or environmental factors could also affect development of larvae but may have minor impact on trunk depth. Therefore, if development time explains integration, we could anticipate a greater correlation between parts that develop at the same time [4]. According to Klingenberg [16], the skull is designed to overcome mechanical forces produced during chewing, capture and processing of prey, respiration, and vocalization. In this sense, Osse *et al.* [53] demonstrated that during initial stages, feeding is a vital process that governs the speed of growth (positive allometric) of the head and all related structures.

The morphological development of larvae seems to be a process in which modularity and integration are two basic strategies [69]. The rate of development could contribute to the ontogenetic patterns detected by variance and integration; *i.e.* a high variance and low integration would be expected in smaller size classes, and a decrease in variance and increase in integration would be expected in mature individuals [67]. Pressure, friction, and resistance to movement are factors that highly depend on shape, because of isometric scaling and increase in mass. Acceleration during bursts and fast-starts may decrease due to an increase in size [70] [71]. However, Gibb *et al.* [59] found that escape performance improved with the development of adult morphology; hence, fish that enter the environment in an advanced development phase should have a greater ability to evade predators than those that enter during an early stage of development. Antonucci *et al.* [72] concluded that in adults the shape of apex predators is similar to the "BCF-transient" type proposed by Webb [73] since they can display a fast start, powerful turns, and powerful propulsion. Propulsion is provided by a long and narrow caudal peduncle. Evolution of uncoupled locomotive systems was an important factor underlying the adaptive radiation of teleosts [74].

The relative importance of the caudal module depth can depend on the context of the predator-prey interaction. The lutjanids are an opportunistic species that belongs to the mid- and top predator category focusing on slow-moving prey (crabs, shrimp & small fish). Adults *L. campechanus* (Poey, 1860) have few predators and their body are elevated depth, narrow caudal peduncle and small eyes [72]. The adult organisms are associated with depressions and high relief structures such as reefs and rocks [21]. During developmental stage, they do not move far from their settlement site [75]. This type of predatory behavior and lifestyle are the reason behind a body shape that is better adapted to sustained and prolonged swimming during its adult stage.

Finally, the size range used in this study was limited to the scale of the first sexual maturity, which is why the effects of variation between the last two classes were not observed. Morphological design for each stage of development reflects a correspondence where performance is optimized according to environmental conditions where they inhabit. In juveniles living in soft bottoms or low shallow areas of open water (<24 m), with moderate to strong currents, the structural complexity is minimal. Its fusiform shape could confer them certain ecological advantages, such as stability in swimming and fast-start performance that would increase their rate of survival in fast moving waters and high exposure to predators. The largest classes live associated with rocks or coral reefs in environments that are steadier; its body shape is deeper and robust designed for sustained swimming necessary for the switch to a more sedentary lifestyle. In future studies, it would be desirable to supplement this information including larger specimens (*i.e.* above 50 cm SL), a size at which this species continues to grow only isometrically [56].

5. Conclusion

This is the first ecomorphological report of *L. campechanus* in Mexico with the aim to identify patterns among morphology, behavioral performance and ecology. This study described the development patterns during ontogenetic growth and change in shape in *L. campechanus* (Poey, 1860) using geometric morphometric techniques. The trend observed during early and young juvenile stages were slightly more streamlined than during adulthood, *i.e.* the modular development processes during growth optimized certain structures of the body (head, body, tail). The development of the head and tail was a fast process occurring between lengths of 3 and 15 cm SL (CL0-CL2), being the head, the module that experienced significant variations in lengths up to 20 cm SL.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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