

## Article

# An Overview of Interlocation Sexual Shape Dimorphism in *Caquetaia kraussi* (Perciformes: Cichlidae) A Geometric Morphometric Approach

Jordan Hernandez <sup>1,\*</sup>, Amado Villalobos-Leiva <sup>2,3</sup>, Adriana Bermúdez <sup>1,4</sup> , Daniela Ahumada-Cabarcas <sup>1,4</sup> , Manuel J. Suazo <sup>5</sup>  and Hugo A. Benítez <sup>2,6,\*</sup> 

<sup>1</sup> Grupo de Investigación en Biología Descriptiva y Aplicada, Programa de Biología, Universidad de Cartagena, Cartagena de Indias 130015, Colombia; abermudezt@unicartagena.edu.co (A.B.); dahumadac1@unicartagena.edu.co (D.A.-C.)

<sup>2</sup> Laboratorio de Ecología y Morfometría Evolutiva, Centro de Investigación de Estudios Avanzados del Maule, Universidad Católica del Maule, Talca 3466706, Chile; avillaleiv@gmail.com

<sup>3</sup> Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Concepción 4030000, Chile

<sup>4</sup> Grupo de Investigación Hidrobiología, Universidad de Cartagena, Cartagena de Indias, Bolívar 130015, Colombia

<sup>5</sup> Instituto de Alta Investigación, Universidad de Tarapacá, Casilla 7D, Arica 1000000, Chile; suazo.mj@gmail.com

<sup>6</sup> Centro de Investigación en Recursos Naturales y Sustentabilidad (CIRENYS), Universidad Bernardo O'Higgins, Avenida Viel 1497, Santiago 8370993, Chile

\* Correspondence: jhernandezm11@unicartagena.edu.co (J.H.); hbenitez@ucm.cl (H.A.B.)



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**Abstract:** *C. kraussii* is an endemic fish species from Colombia and Venezuela and represents a valuable food resource for local human communities. Due to its economic importance, the management and captive breeding of this species are of special interest. However, the anatomical similarities between sexes have been a problem for visual identification. It is also important to indicate that *C. kraussii* has cryptic morphological behavior between sexes, a topic that has been one of the main problems for the implementation of management plans. The following research studied individuals from three different localities along the Canal del Dique, Bolívar Department in Colombia, in which the body shape of *C. kraussii* was analyzed using geometric morphometric analysis. The analyses detected the presence of intralocality sexual dimorphism in two of the three localities analyzed, showing a low morphological variability among males, presenting conserved body shape, as well as a greater morphological disparity among females. This sexual shape dimorphism may be associated with the environmental variation among different locations. These results suggest the presence of two evolutionary forces acting asymmetrically between the sexes of *C. kraussii*, with males mostly subject to sexual selection pressure, while females are mainly subject to environmental pressures.

**Keywords:** geometric morphometrics; Cichlidae; sexual dimorphism; shape; sexual selection

## 1. Introduction

Classifying and understanding the complexity of morphological diversity in organisms have historically been the basis of comparative anatomy. Part of this diversity may be established by natural and/or sexual selection. The sexual selection theory states that selection depends on the fact that individuals of the same species and sex have advantages regarding reproduction [1–3], affecting the success of differential mating [4]. Sexual selection can be intrasexual when males of the same species compete among them to gain access to the other sex, and intersexual selection is related to the differential selection of the opposite sex [5]. The significant difference in size ranges, specifically the body size of a species, between males and females is defined as sexual size dimorphism (SSD) [6–8],

and it is considered one of the main determinants of mating success in many species [9,10]. On the other hand, sexual shape dimorphism (SShD) deals with the comparative analysis of shape between males and females, but it has been less studied. However, in those studies where it was used, it has been proposed as a diagnostic tool for the identification of sex [11,12]. One of the tools used to study shape is geometric morphometrics (GM), which is defined as the geometric information of an object that is retained after removing the effects of translation, scale and rotation [13–15]. In GM, the methods used to determine sexual dimorphism include applying landmarks, defined as specific, equivalent and homologous points in a biological structure being studied, or semilandmarks, which quantify two- or three-dimensional homologous curves and surfaces and are analyzed together with landmarks [9]. GM allows studying the shape of organisms, providing sound graphic analyses based on which morphometric variation can be quantified and visually perceived within and between the samples of organisms [16,17]. Therefore, studying shape differences in individuals in one species or between species is considered to be of scientific interest, since its comprehension may reveal insights about evolutionary stress and the adaptive mechanisms acting upon them [18–20].

A major proportion of sexual dimorphism studies have focused on vertebrates [5]. In particular, teleost fish happen to be an interesting group to study sexual dimorphism [5,21], since they show large intraspecific variation [22]. Some studies, such as Lima-Filho et al. [4], showed the effect of a longitudinal cline on the sexual shape dimorphism of individuals of *Bathygobius soporator* (Valenciennes 1837), showing significant intra- and interpopulation differences in the sexual differentiation of the species. Similarly, Gonzales et al. [23] determined sexual dimorphism in *Rachycentron canadum* (Cobia) (Linnaeus, 1766) in captivity based on the size and shape of individuals; Brzozowski et al. [24] used cichlids from Malawi lake, Africa, in order to determine sexual dimorphism based on the color trait of individuals, and they found significant differences between males and females.

In particular, in the group of freshwater fish, a number of species differ in the expression of sexual traits, such as *Trachelyopterus insignis* (Steindachner, 1878), which shows morphological differences between males and females [25], or the case of the characin *Hyphessobrycon myrmex*, where females are yellow and males are red, as an example of sexual dichromatism [26], whereas, in other species, morphological differences are reduced, such as the case of *Caquetaia kraussii* (Steindachner, 1878), a species endemic to Colombia and Venezuela belonging to the Cichlidae family, commonly named yellow mojarra [27].

In Colombia, *C. kraussii* is considered a species of high commercial relevance [28,29], and it is distributed in the medium and low regions of the rivers Sinú, Cauca, Magdalena, San Jorge, Cesar and Arauca, down to Puerto Berrío, and freshwater or low-salinity marshes with submerged vegetation [27,30].

*C. kraussii* features a yellow or light brown body, with cross stripes in black and a black spot in the upper posterior region of the caudal peduncle and a bigger one in the central part of the body, below the dorsal fin and in the caudal fin [31,32]. This morphology is observed to be very similar between males and females, characters that may indicate that this species has cryptic morphological behavior between different sexes.

Therefore, the aim of this study was to quantify the sexual shape dimorphism of *C. kraussii* by means of advanced morphological tools in order to evaluate whether the geometric shape could identify cryptic morphology related to environmental or sexual dimorphism factors. As a case study, individuals distributed in the “Canal del Dique” and its marsh complex in the Colombian Caribbean were examined.

## 2. Materials and Methods

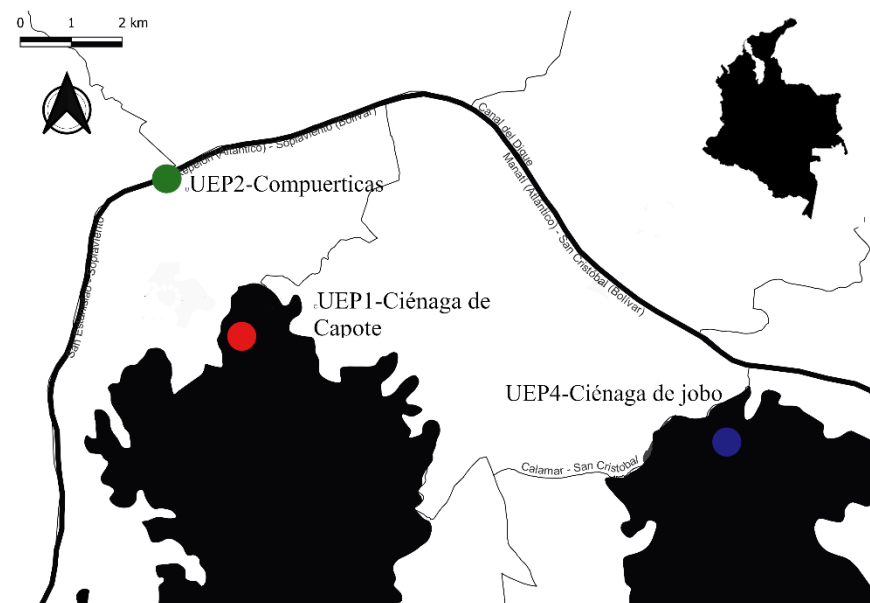
### 2.1. Study Area

The Canal del Dique, located in the Bolívar Department of Colombia, is an alluvial plain formed by a complex of wetlands composed of marshes that soften the Canal flow. The Canal is 113 km long from the town of Calamar to its mouth in Cartagena Bay [33].

## 2.2. Field Work

Field visits were carried out every other month for four days between December 2020 and October 2021, during which fresh *C. kraussii* specimens were collected by artisanal fishing with a cast net and gillnetting along the Canal del Dique and the marshes next to it.

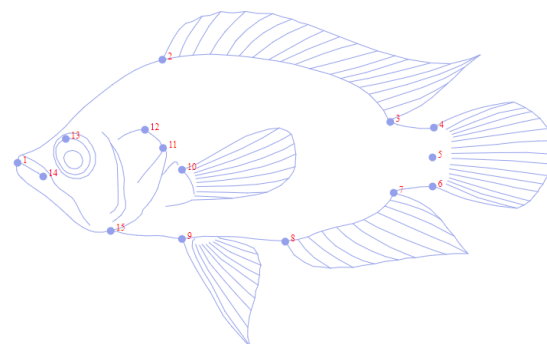
The biological material was sacrificed and identified in situ using the field guide Colombian Andean Fish and the Catalogue of Continental Fishery Resources of Colombia [31,34]. Eighty *C. kraussii* specimens were analyzed from three locations being studied: UEP1—Ciénaga de Capote; UEP2—Canal del Dique/Compuerticas; and UEP4—Ciénaga del Jobo/San Cristóbal (See Figure 1). There were 47 females and 33 males, the sex of which was determined by direct observation of gonads [35].



**Figure 1.** Location of Sampling Points. Zodes Dique (Canal del Dique Subregion: Red: UEP1, Green; UEP2; Blue: UEP4. Source: Author).

## 2.3. Geometric Morphometrics

In order to obtain the images, individuals were fixed with pins and placed on a white Styrofoam base in an anterior–posterior position with fins extended. Additionally, a scale ruler was used to establish the scale when the picture was taken. The photographs were taken with a high-resolution FUJIFILM camera with 24 Megapixels. Landmarks were established following Corti and Crosetti [36], Soria et al. [37] and Aguirre and Jiménez-Prado [38] criteria, and they were digitized and converted into coordinates in a bidimensional plane using the tpsDig2 [39] software. In total, 15 landmarks were identified (Table 1), as shown in Figure 2.



**Figure 2.** Graphical representation of *Caquetaia kraussi* body shape with 15 landmarks.

**Table 1.** Anatomical description of landmarks in *C. kraussii*.

N° Landmarks	Position
1	Upper tip of the mouth
2	First spine of the dorsal region
3	Posterior insertion of dorsal fin
4	Dorsal base of caudal fin
5	Ventral insertion of caudal fin
6	Ventral base of caudal fin
7	Posterior insertion of anal fin
8	First spine anal
9	Anterior base of first pelvic fin ray
10	Superior insertion of pectoral fin
11	Posterior tip of operculum
12	Dorsal border of preoperculum
13	Middle of the eye
14	Cleft of the upper lip
15	Anterior margin of the cleithrum

By means of a Generalized Procrustes Analysis (GPA), the Cartesian coordinates derived from the landmark positions were processed. The GPA superimposes the resulting configurations of all the specimens analyzed, fitting them to a unitary centroid size and eliminating rotation and translation of configurations [14]. The GPA is based on the minimum squares to obtain the optimal superimposition; that is, it averages the lack of fit of all the points, allowing the detection of differences between different configurations. The GPA calculates the average configuration, which summarizes the configurations of all landmarks so that the specimen shape can be described and compared [14,23,40–42]. In the process of determining the landmarks, the measurement error was calculated by digitizing twice the reference points in a sample of individuals and by means of a Procrustes ANOVA; the values of mean squares of individuals were compared to see if they were lower than the error [43,44]. A principal component analysis (PCA) was conducted using the covariance matrix of individual shape [45]. Then, a scatterplot was generated, where the first two shape dimensions were shown graphically. After that, in order to observe the average shape changes for the classifiers (sex and population), a PCA from the covariance matrix of the average combined classifier (population  $\times$  sex) was performed. Then, the body shapes were superimposed onto each other. Finally, with the purpose of highlighting changes associated with the sexual dimorphism of shape between populations, a canonical variate analysis (CVA) was carried out using a combined sex and location classifier. CVA uses the Procrustes coordinates and produces a set of new variables, canonical variates (CVs), which successively account for the maximum amount of among-group variance relative to within-group variance. Moreover, the CVs are uncorrelated within and among groups. It is important to note that CVA is a discriminant analysis that maximizes variation between groups, creating a new shape axis.

To determine the existence of statistically significant differences in SShD, a permutation test was performed (10,000 permutations) using Mahalanobis distances (morphological distances resulting from a CVA). All analyses were conducted with the MorphoJ 1.07a software [46].

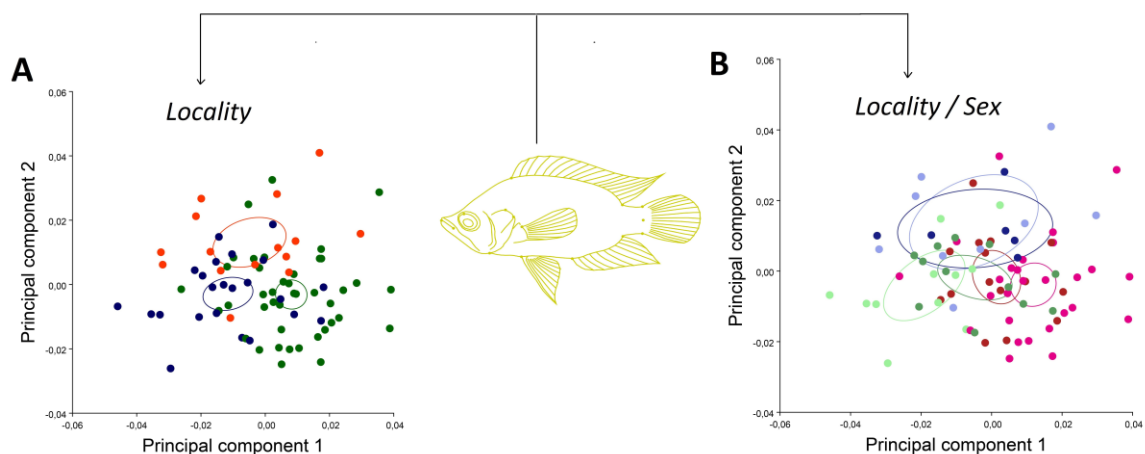
### 3. Results

The Procrustes ANOVA conducted to assess the measurement error showed that the mean square value of individuals was higher than the measurement error (MSerror: 0.0000068573 < MSindividual 0.000077336) (Table 2).

**Table 2.** Procrustes ANOVA for digitizing measurement error of centroid size and shape of *Caquetaia kraussii*.

Centroid Size							
Effect	SS	MS	df	F	P (param.)		
Individual	186.8477	5.049938	37	12.95	<0.0001		
Error 1	14.430189	0.390005	37				
Shape, Procrustes ANOVA							
Effect	SS	MS	df	F	P (param.)	Pillai tr.	P (param.)
Individual	0.07439725	0.000077336	962	11.28	<0.0001	19.65	<0.0001
Error 1	0.00659669	0.000006857	962				

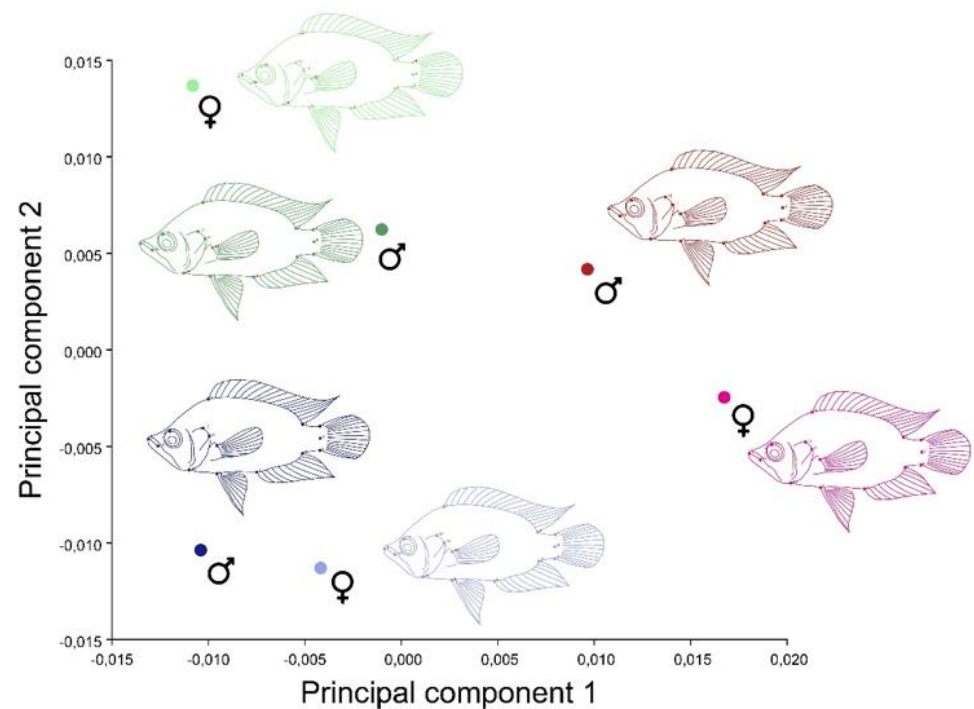
The PCA by location showed that the first three PCs accounted for 50.03% (PC1: 23.9; PC2: 14.3; PC3: 11.7) of shape variation in *C. kraussii* (see Figure 3A). Similarly, the PCA using the sex–location classifier did not reveal large differences in the shape variance between sexes, but it did show a trend in which they become separated by location (Figure 3B).



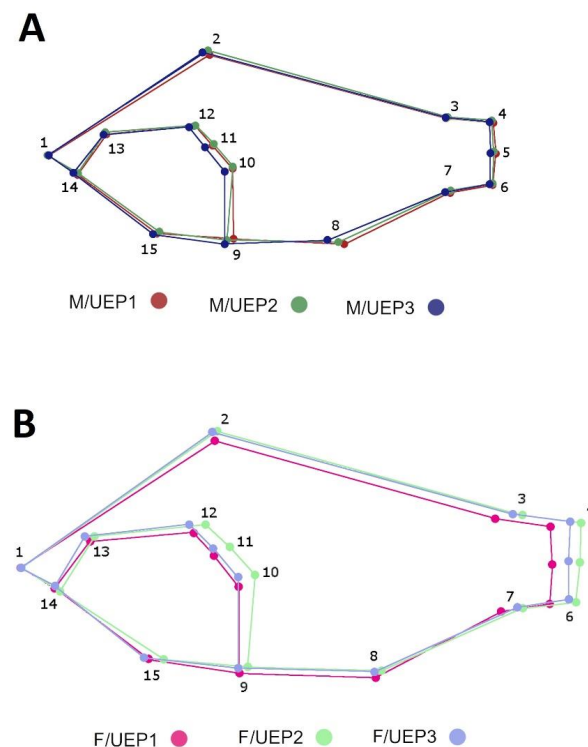
**Figure 3.** Principal component analysis of *Caquetaia kraussii*: (A): scatterplot of shape variation between three localities. Green: UEP1; orange: UEP4; and blue: UEP2. (B): Scatterplot of intralocality sexual shape dimorphism between three localities. Pink: female UEP1; red: male UEP1; light green: female UEP2; dark green: male UEP2; light blue: female UEP4; and dark blue: male UEP4. The confidence ellipses were computed from the mean shape using the criteria locality and locality/sex.

After averaging data, the average PCA (Figure 4) showed a slight shape variation in the body of males between locations; however, it presented slight variations, with a descending displacement towards the ventral area formed by landmarks 10, 11 and 12, which corresponds to the insertion of the pectoral fin, posterior edge of the operculum and the dorsal edge of the preoperculum, respectively.

Likewise, changes associated with the upward movement towards the dorsal area of landmark 8 were observed, corresponding to the first anal spine (see Figure 5A). On the other hand, female shape showed more disparity between locations, where UEP1 and UEP4 populations had a more compact body, although there was a difference because UEP1 females had a shorter caudal peduncle than UEP4 females. On the other hand, UEP2 females exhibited a longer and hydrodynamic shape, with a larger size of the operculum, which is a characteristic of fish in lotic environments (see Figure 5B).



**Figure 4.** Average principal component analysis of *Caquetaia kraussi* representing sexual shape dimorphism among localities. Pink: female UEP1; red: male UEP1; light green: female UEP2; dark green: male UEP2; light blue: female UEP4; and dark blue: male UEP4.

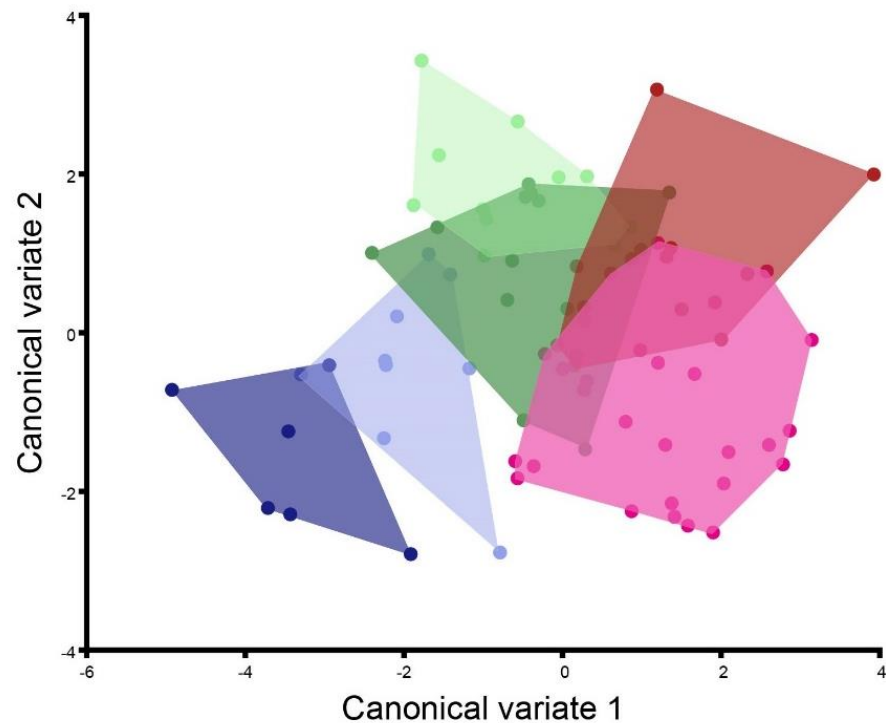


**Figure 5.** Average shape superposition of *Caquetaia kraussi* represented by colored wireframe between sexes and localities. (A): Male Wireframe Overlay. red: male UEP1; dark green: male UEP2 and dark blue: male UEP4. (B): Female's wireframe overlay. Pink: female UEP1; light green: female UEP2 and light blue: female UEP4.

The canonical variate analysis confirmed the presence of the SShD of the *C. kraussi* body, with a clear difference among locations (see Figure 6). Furthermore, these differences



were significant after the permutation test using Mahalanobis distances (Table 3). The only comparison resulting in no significant shape differences was between UEP2 females and UEP2 males.



**Figure 6.** Canonical variate analysis of *Caquetaia kraussi* localities and sex in three populations in Colombia. Pink: female UEP1; red: male UEP1; light green: female UEP2; dark green: male UEP2; light blue: female UEP4; and dark blue: male UEP4.

**Table 3.** Permutation test based on Mahalanobis distances and their corresponding *p*-values of the comparison between populations and sexes of *C. kraussii*.

	H/UEP1	H/UEP2	H/UEP4	M/UEP1	M/UEP2
H/UEP2	3.1459				
<i>p</i> -values:	<0.0001				
H/UEP4	3.3519	3.6005			
<i>p</i> -values:	<0.0001	<0.0001			
M/UEP1	2.2344	3.2729	3.9664		
<i>p</i> -values:	0.0001	<0.0001	<0.0001		
M/UEP2	2.5726	2.014	3.6465	2.7917	
<i>p</i> -values:	<0.0001	0.4495	<0.0001	0.0002	
M/UEP4	4.4469	5.0323	4.2434	5.1425	4.2772
<i>p</i> -values:	<0.0001	<0.0001	0.002	<0.0001	0.0002

#### 4. Discussion

The results of this study show that, although there is slight sexual dimorphism of the geometric shape at the species level in *C. kraussii*, clear intralocation sexual shape dimorphism (SShD) of the body can be observed. *C. kraussii*, along the subregion Canal del Dique, inhabits a great variety of environments, from lentic water bodies (marsh) to lotic environments (Canal del Dique course) [47]. It is also observed that males have a more conserved body shape, with slight variations among the locations studied. Conversely, there is a significant variation in the body shape of females, which may be conditioned by their habitat. Females from both UEP1 and UEP4 have more robust and compact bodies, both being in marsh environments characterized by quiet waters with low current.

The main differentiation is that UEP4 females have a longer tail, which may be efficient for moving in an environment where, although the current is low, it is deeper than the shallow marsh present in UEP1. On the other hand, the body of females inhabiting UEP2 is significantly more acute and longer, and at the same time, their caudal peduncle leans towards the dorsal zone of the caudal fin. The UEP2 habitat is above Canal del Dique; therefore, it is an environment with a strong flow, so the adaptations of females inhabiting UEP2 seem to have occurred in order to have a more hydrodynamic body shape adapted to move freely and with low effort in waters flowing at higher speeds. A similar pattern was reported by Perazzo et al. [48], who found that individuals in lotic environments have a more hydrodynamic shape, as well as a larger operculum.

In this sense, the fact that the body shape of *C. kraussii* males does not have major variations among locations, unlike females of the same species, seems to show the presence of different selective stresses acting in a dissimilar manner between individuals of different sexes within the same species in an interpopulational manner. As described by Hedrick and Temeles [49], the presence of a conserved shape in males among populations would be an indication that the selective stress on males is mainly exerted by females by means of the sexual selection of mates, where certain traits are actively selected over others, causing the male body shape to then be more reserved, with a conserved body scheme between populations. Kodric-Brown and Nicoletto [50] observed a similar pattern in poeciliids such as Guppy (*Poecilia reticulada*) and mosquitofish (*Gambusia holbrooki*). They studied the effect of two components in male mating, the color and exhibition behavior, in the selection by females, and they found that females select their mates based on both static and dynamic traits, showing a preference for the more noticeable males. On the other hand, Ramos Salazar [51] studied the factors that have an influence on females' preference for males in *Gambusia holbrooki* individuals, and they found that females seem to prefer males with a larger size. Another study that supports our result that females may be exerting a degree of sexual selection on males is the one published by Selz et al. [52], who determined that, in cichlid species, there is sexual selection by females at intra- and interspecific levels, revealing that the nuptial coloring is a sexual selection objective by females [53].

On the other hand, body shape variance in females seems to be determined by selective environmental stresses due to both abiotic environmental features and the stress exerted by predators and intersexual competence. Bolnick and Doebeli [54] stated that species with strong selective mating based on ecological traits are less likely to develop sexual dimorphism, which is evidenced in the results of this study, considering that *C. kraussii* does not show many differences between males and females; however, when splitting them by population, dimorphism becomes apparent. In the same manner, it is possible that female shape variation changes due to ecological selection, which, according to Hedrick and Temeles [49] and Herler et al. [5], can have a differential impact on both sexes, favoring dimorphic niches. Their hypothesis suggests that environmental selection acts mainly on females [55], results that were shown by geometric morphometrics in *C. kraussii* females. Badyaev [56] and Lima Filho et al. [4] suggested that physical and ecological conditions of environments can give rise to the evolution of sexual dimorphisms [57,58]. A similar pattern was observed by Stillwell and Fox [59], showing that temperature (an environmental ecological factor) induces sexual shape dimorphism in the seed beetle (*Callosobruchus maculatus*). Regarding fish, Laporte et al. [60] studied the ecology of sexual shape dimorphism in *Salaria fluviatilis*, finding that selective environmental stresses affect sexual selection and, therefore, the visualization of sexual dimorphism within the species.

In addition, it is important to mention that there have been very few sexual shape dimorphism studies using geometric morphometrics. In fish, the sexual dimorphism of shape was studied in Tule perch, *Hysterocarpus traskii*, and significant differences in perch shape were found using GM [61]. Another study was conducted by Saura et al. [62], who, by means of GM, evaluated the fluctuating asymmetry and sexual dimorphism in *Channa striata* individuals; these groups are clear examples of studies where the combination



of high-resolution morphological tools was able to unravel traits in the life history of organisms.

Finally, this study shows evidence for the effects of different selective stresses acting in an asymmetric manner between sexes in *C. kraussii*, as determined by environmental variables along a continuous environment, although heterogeneous. These results are a valuable information source for understanding the adaptative, selective and microevolutionary processes that occur simultaneously along the Canal del Dique basin. Similarly, since *C. kraussii* is a species with value and commercial relevance, this study provides useful information for the creation of management and exploitation plans for this resource, emphasizing considerations about the effect of the morphological variability of females subject to different environmental characteristics, and at the same time, since they have a conserved body shape, the translocation of males between different populations may serve as a strategy to increase the genetic heritage, which is useful information for creating conservation strategies.

**Author Contributions:** Conceptualization, J.H., A.V.-L., A.B., D.A.-C. and H.A.B.; data curation, J.H.; formal analysis, J.H. and H.A.B.; funding acquisition, A.B.; investigation, J.H., A.V.-L., D.A.-C., M.J.S. and H.A.B.; methodology, J.H. and H.A.B.; project administration, A.B.; resources, A.B.; software, J.H.; supervision, H.A.B.; validation, J.H. and H.A.B.; visualization, J.H., M.J.S. and H.A.B.; writing—original draft, J.H., A.V.-L., D.A.-C. and H.A.B.; writing—review and editing, J.H., A.V.-L., A.B., D.A.-C., M.J.S. and H.A.B. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** Ethical review and approval were waived for this study, due to the species under study is not a protected species and is very abundant in the area, moreover, it is widely distributed and traded in sites of interest for this research.

**Data Availability Statement:** Data will be available in supplementary methods.

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