



REPRODUCTIVE SEASONALITY DIFFERS BETWEEN CONTRASTING MORPHOTYPES OF *Megaleporinus obtusidens* (TELEOSTEI: CHARACIFORMES) IN LOWER URUGUAY RIVER

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ABSTRACT

The “boga” (*Megaleporinus obtusidens*) is a fish of great importance in both fisheries and ecology in the Uruguay River with wide phenotypic plasticity and variation in its body morphology. Despite this, little is known about its biology and reproductive ecology. In this study, we evaluate the reproductive dynamics of *M. obtusidens* with contrasting morphologies in the lower Uruguay River. The fish were collected monthly during two years, identifying the morphotype as Morphotype 1 (“elongated body”) or Morphotype 2 (“oval body”) (n=232). Traditional and Geometric Morphometry was used in a subset of specimens to test for morphological differences. Likewise the Gonadosomatic Index (GSI) was estimated and compared between Morphotype 1 and Morphotype 2. Morphometric analysis confirmed the differences between contrasting morphotypes. The two morphs exhibited distinct reproductive patterns: the individuals of Morphotype 2 recorded higher GSI in spring, marking a reproductive peak in November, while the specimens of Morphotype 1 showed no differences in GSI between seasons. This study shows that there are two morphs of *M. obtusidens* found in lower Uruguay River which may represent two different taxonomic units or perhaps two stocks. This should be considered in fisheries management, to attain a more sustainable use of this resource.

Key words: Morphological variation, geometric morphometry, gonadosomatic index, Uruguay River.

RESUMEN

Diferencias de estacionalidad reproductiva entre morfotipos contrastantes de *Megaleporinus obtusidens* (Teleostei: Characiformes) en el bajo Río Uruguay. La “boga” (*Megaleporinus obtusidens*) es un pez de importancia pesquera y ecológica en el río Uruguay con amplia plasticidad fenotípica y variación en su morfología. A pesar de ello, poco se conoce sobre su biología y ecología reproductiva. En este trabajo evaluamos la dinámica reproductiva de *M. obtusidens* de morfologías contrastantes en el bajo río Uruguay. Los peces fueron colectados mensualmente durante dos años, identificándose los individuos como Morfotipo 1 (“cuerpo alargado”) o Morfotipo 2 (“cuerpo ovalado”) (n=232). Se utilizó Morfometría Tradicional y Geométrica en un subconjunto de especímenes para testear diferencias morfológicas. Asimismo, se estimó y comparó el Índice Gonadosomático (GSI) entre morfotipos. El análisis morfométrico confirmó las diferencias entre morfotipos contrastantes. Los dos morfos exhibieron patrones reproductivos distintos: los individuos de Morfotipo 2 registraron GSI más alto en primavera, marcando un pico reproductivo en noviembre, mientras que los especímenes de Morfotipo 1 no mostraron diferencias en GSI entre estaciones. Este estudio muestra que hay dos morfos de *M. obtusidens* encontrados en el bajo Río Uruguay que pueden representar dos unidades taxonómicas diferentes o quizás dos stocks. Esto debería ser considerado en el manejo pesquero, para lograr un uso más sustentable de este recurso.

Palabras clave: Variación morfológica, morfometría geométrica, índice gonadosomático, Río Uruguay.



INTRODUCTION

The “boga” (*Megaleporinus obtusidens*, Valenciennes, 1837) is a species of fish of the Anostomidae family (Characiformes) that inhabits freshwater lotic systems in South America, being frequent and abundant in the inner Río de la Plata estuary, Paraná, Uruguay, and San Francisco River basins (Espinach Ros, 1999; Carolsfeld, Harvey, Ross and Baer, 2003; Ramírez, Birindelli and Galetti, 2017a; Avigliano et al., 2018). It carries out important migrations for food and/or reproductive purposes and, specifically in the Uruguay River, it is the second most important species for commercial, artisanal, and sporting fisheries (Dománico, 2021). In addition, it has recently been highlighted for its great ecological relevance, being the main predator of the Asian golden mussel (*Limnoperna fortunei*) (González-Bergonzoni et al., 2020; 2023), a bivalve that has invaded the Uruguay River since 2001 and has important economic (Boltovskoy, Xu and Nakano, 2015) and ecological consequences for the country and the region (e.g. Cataldo, O'Farrell, Paolucci, Sylvester and Boltovskoy, 2012; Linares, Callisto and Marques, 2017; Duchini, Boltovskoy and Sylvester, 2018; Silva et al., 2021 a,b). Although *M. obtusidens* has been classified as a priority species for conservation in Uruguay (Loureiro, Zarucki, González, Vidal and Fabiano, 2013), its fishing regulation only includes an specific body size restriction (see fishing bans by size, CARU, 2024), with many ecological aspects of this fisheries resource being unknown in Uruguay and the region.

Regarding its morphology, it is known that it is a large species, being able to exceed 70 cm in length and 5 kg in weight. In general, it has an elongated body and its dorsal profile is relatively curved (Britski, Birindelli and Garavello, 2012). Its small mouth has three teeth in each jaw and dentary, being very useful for the ingestion of different prey, due to its omnivorous diet (Hahn, Agostinho, Gomes and Bini, 1998; Hartz, Silveira, Carvalho and Villamil, 2000; González-Bergonzoni et al., 2023). A very relevant aspect, described by local fishermen of the lower Uruguay River and scarcely addressed to date, is the presence of at least two contrasting phenotypes or morphotypes of *M. obtusidens*, which are frequently and abundantly recorded: one with an elongated body and a sub-terminal mouth, called by artisanal fishermen as “elongated boga” and another with an oval body and a terminal mouth, known as “oval boga”. Recently a DNA Barcode approach study found molecular evidence of the existence of the different molecular operational taxonomic units within individuals morphologically identified as *M. obtusidens* along San Francisco and La Plata River basin; however, all the individuals analyzed from middle and higher Uruguay River clustered within the same group suggesting it might represent a single species. Furthermore, Rovira (2017) evaluated whether these elongated body or oval body forms

found in lower Uruguay river are correlated with genetic differences, reinforcing that the different morphological types do not represent different species, but rather an important phenotypic plasticity of a single species, as has been previously reported for other species of *Megaleporinus* (see Bonini Campos, Lofeu, Brandt and Kohlsdorf, 2019). Although this morphological variation is considered and known by the local community, the potential relationships that these phenotypes could have with other biological aspects of great relevance for fish, such as reproduction, have not been studied in depth.

It is well known that body shape and reproduction may be closely linked in many organisms (Zúñiga Vega, Suárez Rodríguez, Espinosa Pérez and Johnson, 2007). However, relatively few studies have attempted to disentangle the cause and effect of these associations (Griffith, 1994; Du and Lu, 2010) and few studies have attempted to assess this association between different phenotypes within the same species (e.g. Višnjić-Jeftić, Lenhardt, Vukov, Gačić, Skorić, Smederevac-Lalić and Nikčević, 2013). According to previous studies in the region (see Felizardo, Murgas, Winkaler, Pereira, Drumond and Andrade, 2011; Andrade et al., 2013; Silva, 2017), the reproductive peak of *M. obtusidens* occurs in spring, concordant with periods of increased temperature and rainfall. The reports of ichthyoplankton and juveniles in the Uruguay River suggest the same pattern, recording maximum densities of larvae and juveniles of *M. obtusidens* towards the end of spring and beginning of summer (Fuentes, Lozano and Vegh, 2017; Mounic-Silva et al., 2017; Cataldo, Leites, Bordet and Paolucci, 2022). However, to date there are no studies that evaluate the reproductive dynamics of adult individuals in the lower Uruguay River, and the potential reproductive differences between phenotypes of this species are still unknown.

Understanding the relationship between morphological variation and reproduction in this species could have important management implications, since they potentially represent different population units with their own reproductive dynamics and could require differential management (Withames and Marshall, 2008). To date, in the Uruguay River, the “boga” fishery is considered as a single stock (Begg and Waldman, 1999). Therefore, underestimating the identification of this stock, without considering potential morphological and reproductive variations, may lead to the loss of subpopulations and consequently of intraspecific biodiversity (e.g. Wudneh, 1998; Viñas et al., 2011).

In this work, we aim to identify and report the existence of two morphotypes of *M. obtusidens* in the lower Uruguay River using traditional and geometric morphometry, that represent efficient approaches to locate morphological differences within the same species (Cadrin and Friedland, 1999; Dwivedi and

Dubey, 2013), and to describe the reproductive dynamics for a two-year period (2021-2023), by estimating the gonadosomatic index, an important metric to evaluate the reproductive status and functional condition of fish because it represents their gonadal development (Vazzoler, 1996).

MATERIAL AND METHODS

Sample collection and laboratory processing

The fish were collected in the town of Las Cañas, Fray Bentos, Río Negro Department, Uruguay (33° 10.452'S, 58° 21.480'W). From March 2021 to March 2023 (approximately every 30 days), up to 20 adult *M. obtusidens* (> 30 cm standard length, according to Quintana, Arbués, Sánchez, González, & Fontana, 2010), or all those caught if that *n* was not reached, were acquired from local fishermen in the area. They were subsequently transferred for laboratory processing.

In the laboratory, each specimen was measured (standard length), weighed, and identified by morphotype, categorizing it as "elongated" or "oval" based on observers perception (Fig. 1) and according to Rovira (2017). In cases where the morphological variation was not clearly identifiable, the specimen was classified as "intermediate". Each specimen was then photographed for subsequent verification of phenotypes through morphometric analysis. Additionally, the lateral line perforated scale count of each specimen was registered and compared between morphotypes, because it is an important diagnosis character between different morphologically similar species within *Megaleporinus* (Britski et al., 2012).

A longitudinal cut was then made at the ventral profile to dissect each individual, identifying the sex (Female, Male), weighing the gonads (with a precision of 0.01 g), and obtaining the eviscerated weight of the animal after removing the viscera.

A total of 307 adult *M. obtusidens* were processed. To disregard any bias given by confusing identification of morphotypes, only specimens with clearly identifiable morphotypes in laboratory processing (contrasting phenotypes) were used in this work ("elongated" or "oval"), discarding data from "intermediate" individuals whose classification could be ambiguous, considering a total of 232 individuals.

Morphometric analysis

To evaluate and verify phenotypic differences found *a priori* in the analyzed specimens, traditional and geometric morphometric approaches were used. Traditional morphometrics combine quantitative morphology and multivariate statistics, analyzing the covariance between variables such as body lengths, widths, and heights (Pietrusewsky, 2018). On the other

hand, the use of geometric morphometrics obtains additional information, allowing the maximum use of the geometric information that a structure has after removing the effects of scale, rotation, and translation of an object. This approach integrates the size of the organisms, providing robust analysis and graphical tools for the quantification and visualization of intra- and interspecific morphological variation (Marcus and Corti, 1996; Adams and Otárola Castillo, 2013).

For this purpose, photographs of a subset of 32 specimens randomly selected along the study period and well differentiated into morphotypes were used: 16 "elongated" (hereafter "Morphotype 1") and 16 "oval" (hereafter "Morphotype 2") considering both sexes.

For the traditional morphometric analysis, seven linear morphological measurements were used, standardized by standard length in order to reduce the effect of differences in body size (Gatz, 1979; Winemiller, 1991), through the digitalization of images of each specimen using the *ImageJ* program version 3.5.2 (Rueden et al., 2017). The measurements taken were: M1: Body height, M2: Pre-dorsal length, M3: Pre-pelvic length, M4: Pre-anal length, M5: Pre-ocular length, M6: Eye diameter and M7: Head length.

With the obtained matrix, a Principal Component Analysis (PCA) followed by a PERMANOVA ($\alpha=0.05$) (Anderson, 2014; Greenacre et al., 2022) was performed to establish the patterns of morphological variation within the multivariate space. This analysis was performed using the *vegan* package and the *adonis2* function in R Software.

For the geometric morphometric analysis, the photographs of the selected specimens were digitized using the *TPSDig232* program (Rohlf, 2017) locating 17 morphological landmarks for each individual, taking into account that the selection described those structures of interest to externally identify the individuals (see Sidlauskas, Mol and Vari, 2011): (1) Anterior limit of the premaxilla, (2) Dorsal tip of the ascending process of the premaxilla, (3) Posterodorsal tip of the supraoccipital, (4) Origin of the first ray of the dorsal fin, (5) Insertion of the last ray of the dorsal fin, (6) Origin of the adipose fin, (7) Posterior extension of the vertebral column and anterior of the hypural plate (end of the body), (8) Insertion of the last ray of the anal fin, (9) Origin of the first ray of the anal fin, (10) Origin of the pelvic fin, (11) Origin of the pectoral fin, (12) Ventral limit of the articulation between contralateral cleithra, (13) Anterior limit of the orbit, (14) Dorsal limit of the orbit, (15) Posterior limit of the orbit, (16) Ventral limit of the orbit and (17) Articulation between the basioccipital and the first vertebra of the Weberian apparatus (Fig. 2).

Subsequently, the data obtained were entered into the *MorphoJ* software (Klingenberg, 2011), to align and rescale these marks using generalized Procrustes analysis. This analysis eliminates information that is not related to shape, including size and position of the specimens. A PCA of the morphometric data was

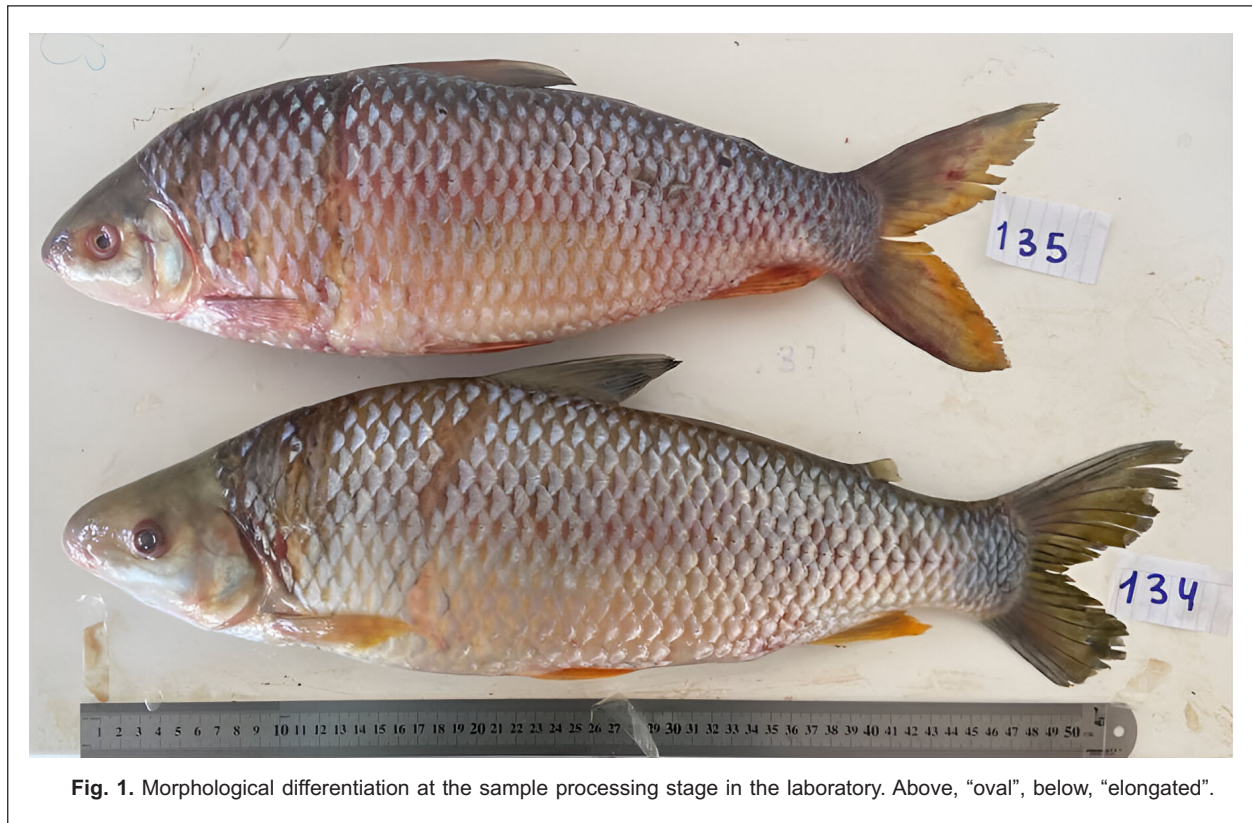


Fig. 1. Morphological differentiation at the sample processing stage in the laboratory. Above, “oval”, below, “elongated”.

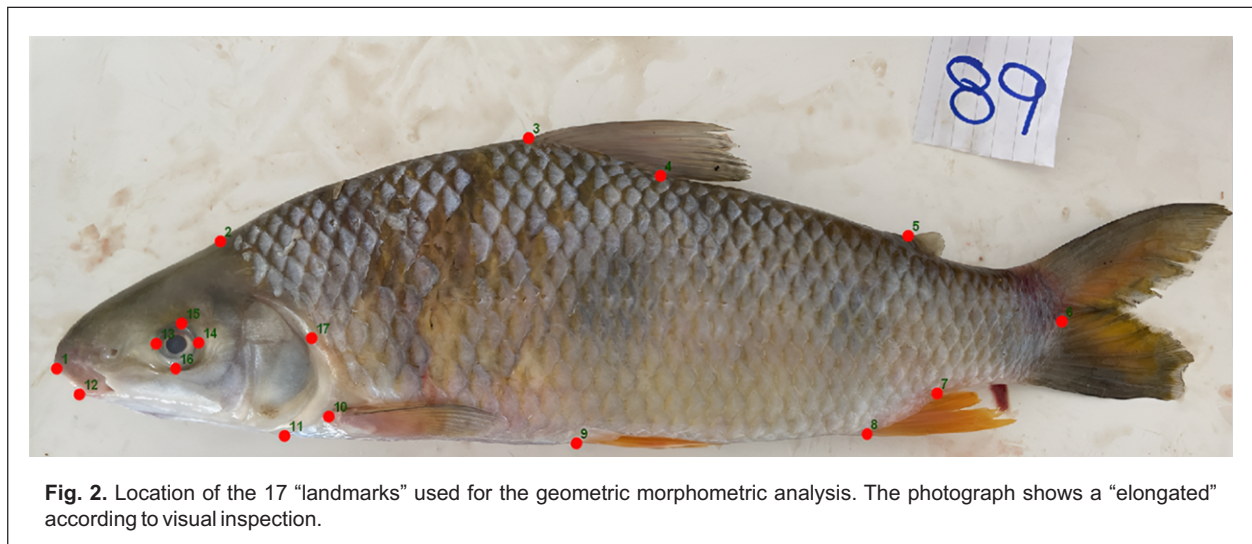


Fig. 2. Location of the 17 “landmarks” used for the geometric morphometric analysis. The photograph shows a “elongated” according to visual inspection.

performed on a covariance matrix. Then, possible shape differences were analyzed using canonical variate analysis (CVA, $\alpha=0.05$) (Klingenberg 2011; Mitteroecker and Bookstein, 2011), obtaining a p value from the permutation test with 10,000 replications with Euclidean squared distance as a measure of dissimilarity. Procrustes distances (denoting the dissimilarity in shape between two landmark configurations) were also extracted in the CVA analysis

to explore the degree of morphological differences between the studied phenotypes.

Reproductive status analysis

To evaluate the temporal reproductive dynamics of *M. obtusidens* in the study area and the possible differences between contrasting morphotypes, the complete data set ($n= 232$) was used. After sex

identification, the gonadosomatic index (GSI) of each specimen was estimated, calculated as:

$$\text{GSI} = \left[\frac{\text{weight of the gonads}}{\text{weight of the eviscerated specimen}} \times 100 \right]$$

For each phenotype, the gonadosomatic index was compared between seasons using individuals as replicates (SU: summer, A: autumn, W: winter and SP: spring) for females and males separately. These comparisons were made by adjusting linear models (LM, $\alpha=0.05$) using the GSI as a response variable and the seasons as a predictor variable. In case $p < 0.05$, the Tukey post hoc test was used to evaluate between which stations the differences are found. Previously, the goodness of fit of the normal and lognormal distributions to the continuous response variable was tested using the “*fitdist*” and “*gofstat*” functions of the “*fitdistrplus*” package (Delignette Muller & Dutang, 2015), with the normal distribution providing the best fit. The variance homogeneity in the modelled data was further confirmed by inspecting at potential patterns in model residuals (Zuur, Ieno and Elphick, 2010. All models were fitted using R (R Core Team, 2024).

RESULTS AND DISCUSSION

Of the 307 individuals processed in the laboratory, a subsample of 32 specimens with contrasting morphological characteristics (16 representatives of Morphotype 1 and 16 of Morphotype 2, was used for morphometric analysis. An attempt was made to select specimens from the entire study period and of both sexes (8 females and 8 males for each morphotype). The average size for the specimens of Morphotype 1 was 40.2 ± 4.2 cm and for the specimens of Morphotype 2 it was 37.2 ± 4 cm. The total average weight was 1468 (± 400) gr for Morphotype 1 and 1154 (± 391) gr for Morphotype 2. To analyze reproductive aspects, 232 specimens with contrasting morphotypes were used; the details of the sizes, weight, sex and morphotype of these fish are indicated in Table 1.

Morphological variation

The results of PCA with traditional linear measures indicated that there are significant differences between the contrasting phenotypes considered (PERMANOVA, $p=0.001$) (Fig. 3). The first two components explained 76% of the variance indicating that the measures chosen are effective to determine these morphotypes, in addition to showing that the visual differentiation in the laboratory was correct. PC1 explained 43% of the variance and the variables that contributed most to the separation of morphotypes were M7: Head length, M5: Pre-ocular length and M3: Pre-pelvic length. PC2 explained 33% of the variance and the most important variables were M4: Pre-anal length, M2: Pre-dorsal length and M1: Body height.

Regarding the geometric morphometric analysis, similar results to those obtained by traditional morphometry stand out. The dispersion diagram of the PCA (after Procrustes) showed significant morphological variation. The first 2 principal components explained most of the shape variation (60%): PC1 explained 41% while PC2 explained 18%. The results of the CVA also showed a separation between the phenotypes of “boga” through their shape (Fig. 4, p -value < 0.001 , Procrustes distance: 0.034). The main differences between morphotypes described by CV1 were given by the landmarks: anterior limit of the premaxilla (1), origin of the adipose fin (6), origin of the first ray of the anal fin (9) and posterodorsal tip of the supraoccipital (3).

It is important to highlight that the number of lateral line scales was different between the subset of contrasting morphotypes considered (LM, $p=0.0053$). Individuals of Morphotype 1 presented 42 scales on average (minimum of 41 and maximum of 43) and those of Morphotype 2 presented 41 on average (minimum of 40 and maximum of 43). This represents an indication that we used exclusively specimens of *M. obtusidens* and not fish of very similar species morphologically such as *M. piavussu*, which is characterized by having between 39-40 scales (see Britski et al., 2012). Furthermore, since i) we found only a few specimens of Morphotype 2 with 40 scales ($n=6$); ii) we did not find other diagnostic characteristics of *M. piavussu*; iii) *M. piavussu* is not reported for Uruguay (see Loureiro, González Bergonzoni, Teixeira de Mello, 2023); and iiiii) *M. obtusidens* from the Uruguay River was not used as reference material in the previous description of *M. piavussu*, we reaffirm that the fish considered here belong to *M. obtusidens*, and there may be specimens with 40 scales, unlike what was observed by Britski et al. (2012). However, since genetic approaches were not considered in this study, we cannot ignore the fact that it is also feasible that Morphotype 2 may potentially belong to the molecular organizational taxonomic unit called “*M.cf. piavussu* lower Paraná” described by Ramírez et al. (2017b), and that therefore, we are dealing with two different cryptic species; an aspect that can only be confirmed by molecular research in future investigations.

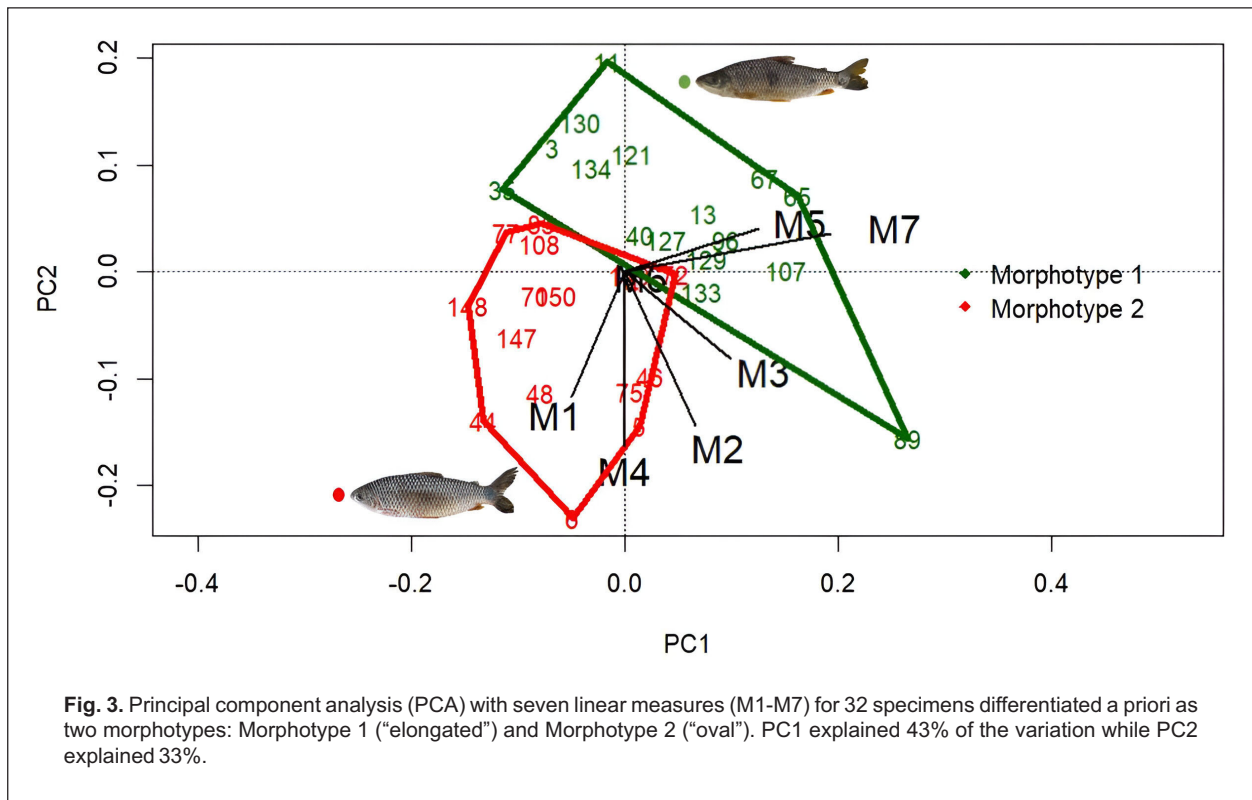
In summary, the morphometric analysis showed that the contrasting phenotypes of the lower Uruguay River *M. obtusidens* are, to a large extent, morphologically distinct entities, which can be easily distinguished at the time of collection (as was done in this study) and corroborated in the laboratory, taking linear measurements that are easy to estimate as well as using novel approximations such as geometric morphometry. This facilitates the recognition of specimens at the time of fishing. However, despite the fact that they were not considered in this study, it is worth noting that 24% of the collected specimens were not classified as “elongated” or “oval”, given their

Table 1. Number (n) and size range (cm) of specimens identified as females and males of each morphotype and on each collection date (the season is indicated in parentheses, SU=Summer, A=Autumn, W=Winter, SP=Spring).

Date	Morphotype 1 (n=155)				Morphotype 2 (n=77)			
	n	FEMALE Size range (cm)	n	MALE Size range (cm)	n	FEMALE Size range (cm)	n	MALE Size range (cm)
9/3/2021 (SU)	3	40-42.5	3	33.5-46	2	37-43	3	31.5-33
26/4/2021 (A)	3	38-45	5	40-46	5	39-50	3	37-38
9/6/2021 (A)	2	39.5-44	1	45	3	38-43	1	38.5
28/6/2021 (W)	2	37-38	2	36-38	5	34-35	3	35-37
2/8/2021 (W)	2	36.5-37	-	-	4	34.5-38	-	-
13/9/2021 (W)	4	38.5-41.5	3	39.5-45	-	-	1	36
8/10/2021 (SP)	8	37.5-45	4	42.5-44	1	36.5	-	-
12/11/2021 (SP)	5	42.5-47.5	2	42	2	40-40.5	2	37-42
30/11/2021 (SP)	3	42-50.5	1	37.5	1	38	-	-
11/1/2022 (SU)	7	40-48.5	10	39.5-46	3	33.5-39	-	-
8/2/2022 (SU)	6	35.8-44.5	2	38.5-40	1	37	2	32-36.5
23/3/2022 (A)	4	43-46	5	41-43.5	4	35-44	-	-
27/4/2022 (A)	4	36-44.5	7	37.5-41	3	39.5-42	-	-
27/5/2022 (A)	5	39.5-44	2	41-43	2	35-40	2	36.5-38
27/6/2022 (W)	1	36	3	38-43	2	38.5-39	-	-
29/7/2022 (W)	2	39.5-44.5	3	40-41	-	-	1	32.5
27/8/2022 (W)	1	40	4	39-43.5	-	-	-	-
15/9/2022 (W)	1	44	-	-	4	38.5-45	-	-
17/10/2022 (SP)	10	40.5-49	-	-	-	-	-	-
22/11/2022 (SP)	5	45-48.5	-	-	5	37-41	2	40-41
12/12/2022 (SP)	5	35.5-45	1	41.5	2	35.5-36	1	42
22/2/2023 (SU)	3	39-44	3	43-44	3	35-43	3	37
23/3/2023 (SU)	1	47	7	43-48	1	40	-	-
TOTAL	87		68		53		24	

variable appearance. We maintain that "intermediate" specimens should be included in future morphometric (and genetics) analyses to assess the relationship with contrasting morphs and whether this implies (or not) different ecological behaviors. The development of different phenotypes of the same species may be the result of the combination of different environmental signals that influence plastic responses (Sidlauskas and Vari, 2008; Machado Evangelista, Esgúlcero, Arcifa and Pereira, 2015). A recent study using larvae and juvenile *Megaleporinus macrocephalus*, revealed for example, that under experimental conditions, the specimens exhibited morphological differences (e.g. mouth and fin position) when the position of the available food changed (Bonini-Campos et al., 2019). Here, although trophic aspects were not considered, it is important to highlight that local fishermen of the lower Uruguay River directly relate the two forms of *M. obtusidens* with differences in their diet: according to personal observation from fishermen, the individuals of

Morphotype 1 would be specialized in the consumption of golden mussels, an abundant food and available in the area for decades, and the specimens of Morphotype 2 would correspond to the generalist omnivorous guild, consuming plant remains, bivalves, gastropods, among others. Although these assumptions have not been explored to date, previously, González-Bergonzoni et al. (2023) established that after several years of colonization of the Asian golden mussel in the Uruguay River, *M. obtusidens* specialized in its consumption and exhibited a marked reduction in the mass of its digestive tract as a plastic response. That said, it would be very interesting to evaluate the trophic ecology of the two morphotypes presented here, given that the availability of resources could be an environmental signal that partly explains the morphological differentiation exhibited by this species, contributing to generating empirical evidence in this regard.



Reproductive dynamics

Of the 232 specimens processed, 155 individuals of Morphotype 1 and 77 of Morphotype 2 were identified. The individuals of Morphotype 1 were collected in all collection months, while the individuals of Morphotype 2 were not collected in August and October 2022 (Table 1). For the specimens of Morphotype 1, 87 females (recorded in all collection months) and 68 males (not recorded in August 2021, September–November 2022) were identified. The *M. obtusidens* of Morphotype 2 were 53 females (not recorded in September 2021, July–August and October 2022) and 24 males (found only on 12 of the 23 collection dates) (Table 1).

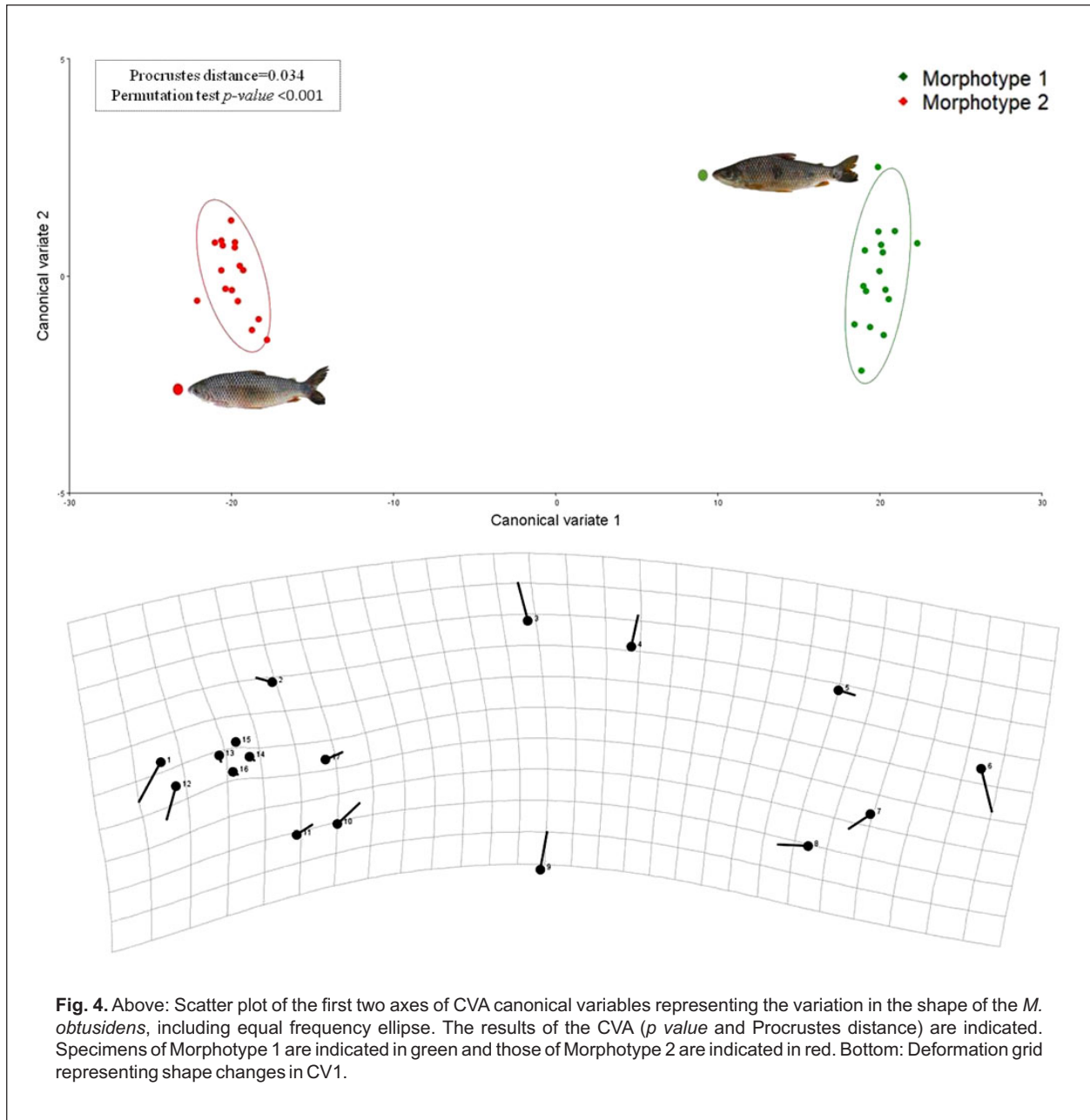
The GSI of individuals of Morphotype 1 was not different between seasons for both females and males (LM, $p=0.44$ and $p=0.07$, respectively) (Fig. 5). However, for Morphotype 2, the GSI of females exhibited a clear pattern, different between seasons (LM, $p<0.001$), being higher in spring, compared to the other seasons (Fig. 5). For males, the differences between seasons were not significant (LM, $p=0.09$) although a tendency to increase GSI was also recorded in spring (Fig. 6).

For the Morphotype 1 and considering only females (given their relative dominance throughout the period) the maximum GSI value was 0.65 and was recorded in June 2022, while the minimum (0.106) was recorded in March 2021 (Fig. 6). In contrast, the Morphotype 2

showed a marked pattern, recording for females the maximum GSI value in November 2022 (8.78) with similar values also in November 2021, indicating reproductive peaks in the spring months. The minimum GSI value for females was 0.31 and was recorded in June 2022 (Fig. 6).

The reproductive pattern of individuals of Morphotype 2 during the study period in the lower Uruguay River is consistent with what was previously recorded for this species in other rivers in the region such as the Paraná or Río Grande (see Felizardo et al., 2011; Andrade et al., 2013; Silva, 2017). The maximum GSI values for this phenotype, coincided with visually mature gonads in immediate pre-spawning and /or post-spawning period and reflected the high gonadal development that the females showed in the months of November–December, suggesting that these fishes use the study area as a reproductive site, consistently with the high abundances of larvae and juveniles of this species in December–February recorded in other works in the same study site (e.g. Fuentes et al., 2017; Mounic-Silva et al., 2017).

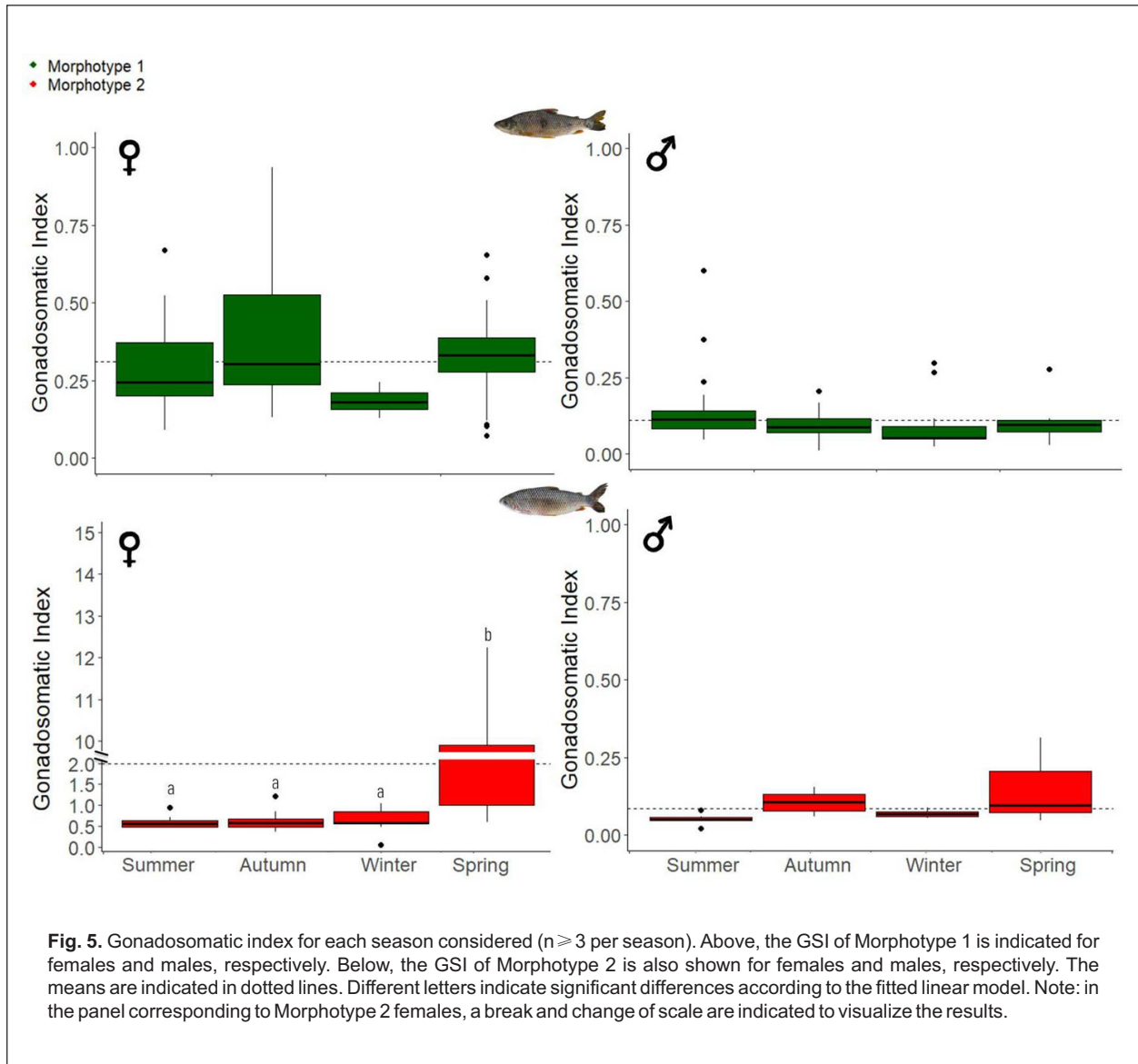
On the other hand, the specimens of Morphotype 1 did not exhibit a clear reproductive pattern, with low GSI values that were not different between collection seasons, and gonads were never visually mature enough to consider that females were pre-spawning or post-spawning. This suggests that the individuals of this morphotype probably do not use the study zone for



reproduction, and may perhaps migrate for this purpose, as has been suggested in previous studies (Andrade et al., 2013). However, Avigliano et al. (2018) using otolith elemental signatures showed a clear spatial segregation both in early life stages and adult stages of *M. obtusidens* collected in Rio de la Plata, Paraná and Uruguay rivers.

The presence of two morphotypes of *M. obtusidens* in the lower Uruguay River, related to two different reproductive strategies suggested here, indicates that many ecological aspects of this species should continue to be investigated, since they imply a necessary input for conservation strategies and sustainable use of this resource of fishing importance

for the area. The existence of these two different units with contrasting reproductive ecology, altogether with previous evidence also suggesting different units within this so called “population” of *M. obtusidens* (e.g. Avigliano et al., 2018) highlights that fisheries management needs to consider the different stocks of groups more precisely. In this work we suggest that knowledge of the existence of both morphs in the Uruguay River should be considered by fishery regulation actors in the area, for example, through fishing bans for Morphotype 2 during its potential reproductive period, in the spring months.



CONCLUSIONS

The report of the two morphotypes of the *M. obtusidens* in the lower Uruguay River represents a fundamental input for the advancement of knowledge on the ecology of this species, acquiring even more importance due to its migratory nature and great commercial relevance. The morphological variations presented here and their relationship with different reproductive strategies suggest that these two forms would represent at least two distinct subpopulations of this species, which should be managed differently, emphasizing the use of this resource in a sustainable way in this river, particularly in times when individuals are at their most vulnerable stage.

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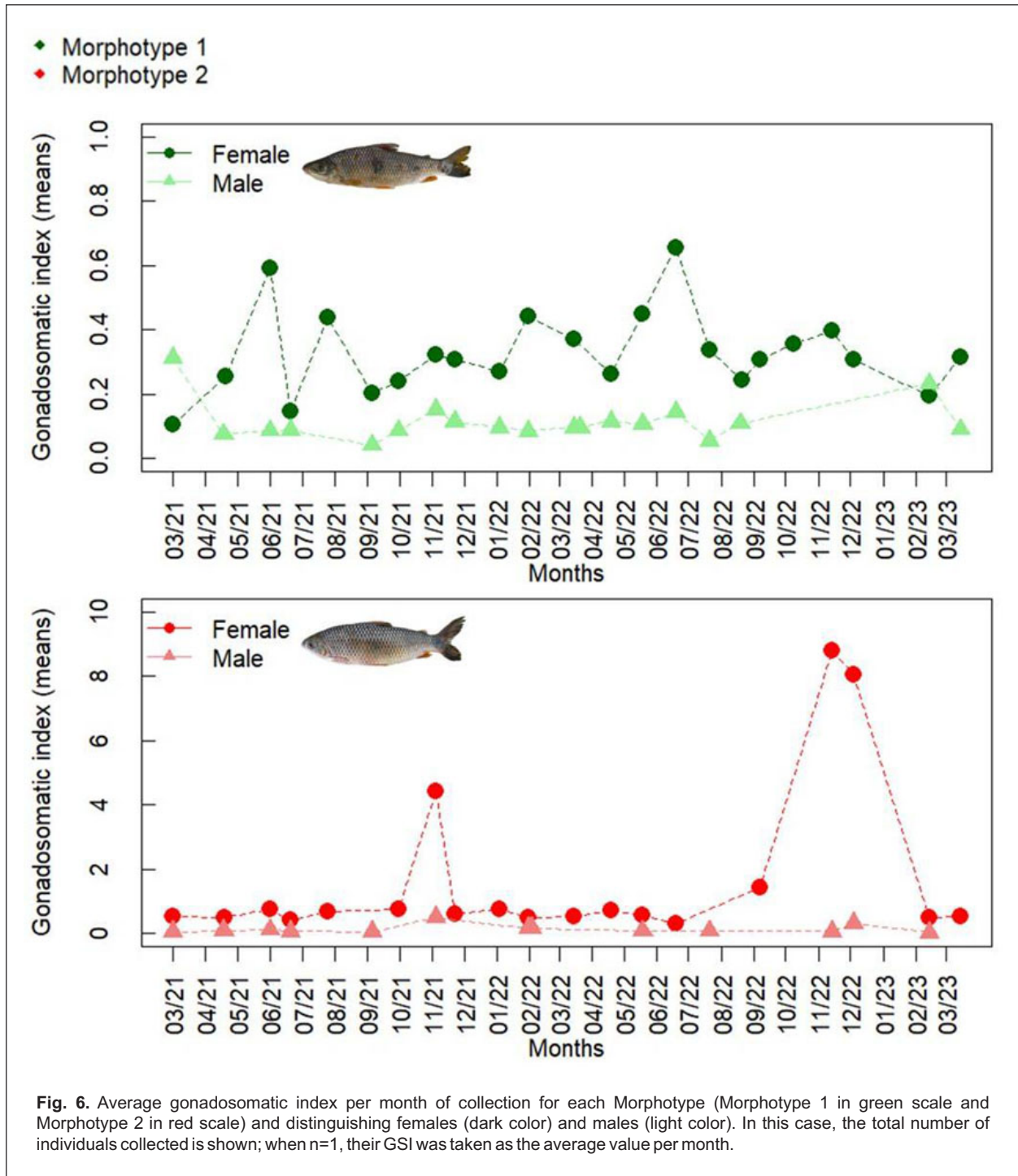


Fig. 6. Average gonadosomatic index per month of collection for each Morphotype (Morphotype 1 in green scale and Morphotype 2 in red scale) and distinguishing females (dark color) and males (light color). In this case, the total number of individuals collected is shown; when $n=1$, their GSI was taken as the average value per month.

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