Latin American Journal of Aquatic Research, 50(3): 417-429, 2022
DOI: 10.3856/vol50-issue3-fulltext-2817

Research Article

Gonadal development, sex ratio, and length at sexual maturity of white mullet *Mugil curema* (Actinopterygii: Mugilidae) inhabiting southeastern Gulf of California

Nurenskaya Vélez-Arellano[1,2], Rebeca Sánchez-Cárdenas[1], Luis Antonio Salcido-Guevara[1] Jorge Saul Ramirez-Perez[1] & Irene Marlen Soberano-Palomares[1,3]

[1]Facultad de Ciencias del Mar, Universidad Autónoma de Sinaloa, Mazatlán, México
[2]Programa Estancia Postdoctoral, Consejo Nacional de Ciencia y Tecnología, México
[3]Programa de Maestría en Ciencias en Recursos Acuáticos, Universidad Autónoma de Sinaloa Mazatlán, México
Corresponding author: Luis Antonio Salcido-Guevara (lsalcido@uas.edu.mx)

ABSTRACT. Research on populations of the family Mugilidae is necessary for the framework of their good use and conservation, given the documented spatial-temporal variation in their attributes and biological processes. *Mugil curema* has also shown particularities in the southeastern Gulf of California, which should be considered. In total, 626 individuals were collected from February 2015 to August 2016. The gonad development pattern was asynchronous and divided into six ovarian and five testicular phases. The sex succession as size increases, the presence of only males in smaller sizes, some aspects of the ovarian structure, and the eosinophilic cells in the ovarian stroma suggest that *M. curema* could be a protandrous hermaphroditic species. Thus, the size at sexual maturity was smaller in males (18.26 cm in total length) than in females (22.08 cm). This information is greatly relevant for fishery management measures and the sustainable use approach and, at the same time, arouses interest in future research.

Keywords: *Mugil curema*; gametogenesis; oocyte stages; gonadal phases; L_{50}, reproductive pattern

INTRODUCTION

The species of the family Mugilidae represent one of the main resources in commercial estuary fisheries in temperate and tropical regions of the world (Blaber 1997). The white mullet or lebrancha *Mugil curema* Valenciennes, 1836, inhabits lagoons, estuaries, and coasts along the subtropical and tropical regions. Its distribution ranges from California, USA, to Chile in the eastern Pacific Ocean. In contrast, in the western Atlantic Ocean, its range goes from Cape Cod, USA, to Brazil (Castro-Aguirre 1978), including the Gulf of Mexico (Robins et al. 1991) and a small population in Africa (Durand et al. 2012). The white mullet forms part of the coastal fisheries in Mexico -the Mexican Pacific, Gulf of California and Gulf of Mexico- (Vasconcelos-Pérez et al. 1996, Briones-Ávila 1998, Meléndez-Galicia & Romero-Acosta 2010).

Fish reproductive characteristics are very important inputs in fish stock assessment and management because various measures rely completely upon the reproductive characteristics of stocks (Tsikliras et al. 2013), and reproductive biology determines productivity. Some works describing the reproductive aspects of *M. curema* in different parts of the world have demonstrated spatial-temporal variations in its reproductive processes and attributes. Gonadal development has been studied mainly from gonadal phase scales based on fresh examination (Lucano-Ramírez 1991, Chávez-Herrera 1993, Lucano-Ramírez & Michel-Morfin 1997, Marín et al. 2003, Cabral-Solís et al. 2010, Meléndez-Galicia & Romero-Acosta 2010, Franco de Oliveira et al. 2011, Ibáñez-Aguirre & Colin 2014). Ovary development has been defined in more detail using histological analyses, from which the following phases have been identified according to dif-

Corresponding editor: Enrique Dupré

ferent authors: resting, early and late development, maturity, partially spent/redeveloping, and spent in the Gulf of Paria (Solomon & Ramnarine 2007); immature, developing, maturing, ripe/running ripe, spent and recovering/resting in Sepetiba Bay, Rio de Janeiro, Brazil (Albieri 2009, Albieri et al. 2010 a,b); immature, maturing, mature and spent in the northeastern region in Brazil (Rocha de Oliveira et al. 2011); immature, maturation, mature, hydrated and spawned in coastal systems in southeastern Brazil (Fernandez & Dias 2013); immature, developing, mature and spawning in Baja California Sur, Mexico (Salgado-Cruz 2020). Furthermore, ovaries have shown a group-synchronous development pattern and spawn multiple batches (Solomon & Ramnarine 2007, Albieri 2009, Albieri et al. 2010a,b, Rocha de Oliveira et al. 2011, Fernandez & Dias 2013, Ruiz-Ramírez et al. 2017, Salgado-Cruz 2020). In contrast, testicular development has been briefly described histologically by Salgado-Cruz (2020) from immature, early development, late development, and spawning capacity phases. Notably, the number of phases and nomenclature to describe gonad development in *M. curema* varies, so little knowledge exists on testicular development.

Sexuality has been scarcely dealt in *M. curema*, and some works have mentioned it as a gonochoristic species without a histological study (e.g. Chávez-Herrera 1993, González-Castro & Minos 2015) despite the sex composition structures by sizes have reported characteristic for protandrous species (Sadovy & Shapiro 1987) with the predominance of males in smaller sizes and female in longer size (Ibáñez-Aguirre et al. 2006, Franco de Olivera et al. 2011, Ruiz-Ramírez et at. 2017, Salgado-Cruz 2020, Salgado-Cruz et al. 2021). Additionally, size diversity at sexual maturity (L_{50}) estimations have been documented from different methods, using different size intervals and criteria to distinguish juveniles from adults. A general trend in L_{50} estimates is that males start sexual maturity at smaller sizes than females, with few exceptions. For example, some authors have reported 24 cm total length (TL) in both sexes in northeastern Venezuela (Baumar & Dodson 2000); 27.8 cm TL in males and 27.4 cm TL in females in Tamiahua Lagoon, Mexico (Ibáñez-Aguirre & Gallardo-Cabello 2004); 25.5 cm TL in females and 27 cm TL in males in Lagoon of Cuyutlan, Mexico (Cabral-Solís et al. 2010); 24.5 cm TL in both sexes in coastal Michoacan, Mexico (Meléndez-Galicia & Romero-Acosta 2010); 26.4 cm TL in males and 24 cm TL in females in Potengi River estuary, Brazil (Franco de Oliveira et al. 2011); 24.3 cm TL in females in Atlantic coastal waters, northeastern region, Brazil (Rocha de Oliveira et al. 2011); 24.86 cm TL in both sexes in coastal systems in southeastern Brazil (Fernandez & Dias 2013); 21.7 cm TL in males and 24.5 cm TL in females in coasts of Jalisco, Mexico (Ruiz-Ramírez et al. 2017); 30.3 cm TL in males and 33.4 cm TL in females in Magdalena Bay, Mexico (Salgado-Cruz 2020); 32.5 cm TL in males and 33 cm TL in females in La Paz Bay, Mexico (Salgado-Cruz 2020, Salgado-Cruz et al. 2020).

Considering the lack of knowledge of *M. curema* in the southeast of the Gulf of California and the variety of reproductive aspects mentioned above, decision-making on fisheries management and conservation of species in the region has high intrinsic uncertainty, representing a risk for the good use of its resources and the sustainability of the population.

Therefore, specific studies in this zone should be performed. In this sense, this research shows gonad development, sex ratio, and length at sexual maturity. These contributions include novel aspects of the reproductive biology of this species of great relevance for fishery management and, simultaneously, arouse interest for future research.

MATERIALS AND METHODS

Weekly random samplings were performed along the coastline of Mazatlan, Sinaloa, Mexico (23°10'N, 106°24'W to 23°19'N, 106°30'W) from the commercial catch of *Mugil curema* for 18 months (February 2015 to August 2016). TL (±1 mm) and total weight (TW) of the individuals (±1 g) were measured in the fishing area. Subsequently, specimens were dissected to extract and weigh the gonads (WG) (±0.01 g). The gonad samples were fixed in 10% formalin solution and processed in the laboratory with the histological technique of dehydration and inclusion in paraffin. A microtomy of 5 μm was performed, and hematoxylin-eosin stain (HE-stain) was applied (Humason 1979).

Slides were photographed, and cell structures were measured from digital images using the program Sigma Scan Pro version 5 (Broomfield, CO, USA). Oocyte diameter (*D*) was estimated by resulting average from the greatest axis diameter and the smallest one for 3358 oocytes (Ruiz-Ramírez et al. 2017) to describe the oocyte size in general (axis-method). Additionally, the diameter of ~30 oocytes per stage was estimated based on the perimeter (*Pr*) from the equation $D = Pr/\pi$, assuming a circular shape of the oocytes (perimeter-method) and also with the axis-method, only to compare the measures between methods. The estimations were compared between methods by the Kruskal Wallis test and the *post-hoc* of Duncan's multiple range test with a significance level of $\alpha = 0.05$ (Zar 2010).

According to Marza (1938), the ovarian development pattern classification was defined from histological observations. A modification of Greeley et al. (1987) technique was also applied, in which total oocytes were counted in a transversal cut (*Nto*) from 3-6 ovaries per gonadic phase, distinguishing the number of oocytes per stage (*n*). Then, the numerical index (*NI*) was calculated for each oocyte stage per gonadic phase, using the equation $NI = \left(\frac{n}{Nto}\right) \times 100$ taken from Pianka (1973). The average *NI* per stage was estimated and graphed in each gonadal phase.

The histological description was performed considering cellular and tissue characteristics, such as oogenesis and spermatogenesis germ cell stages, ovary and testicle wall thickness, and presence/absence of the post-ovulatory follicles and atresia based on the descriptions of Wallace & Selman (1981), Parenti & Grier (2004), Solomon & Ramnarine (2007), Schulz et al. (2010), Brown-Peterson et al. (2011), Lowerre-Barbieri et al. (2011), Fernandez & Dias (2013) and Maldonado-Amparo et al. (2017). In addition, the gonadosomatic index (*GSI*) was calculated by the equation $\mathrm{GSI} = \mathrm{GW}/\ (\mathrm{TW} - \mathrm{GW}) \times 100$ (DeVlaming et al. 1982, Ruiz-Ramírez et al. 2017).

The sex of all collected individuals (n = 626) was confirmed with the histological analysis. The ratio of males per one female (n:1) was estimated by dividing the number of males by the number of females (Cabral-Solís et al. 2010) from the total sample and by size interval of 1 cm. The sex ratio (n:1) observed was compared with an expected ratio of 1:1 from a chi-squared test (χ^2) considering a significance value of α = 0.05 (Zar 2010). The TL structure between sexes was compared using the Kolmogorov-Smirnov test with a significance of α = 0.05 (Zar 2010).

Size at sexual maturity (L_{50}), or the size at which 50% of individuals are adults, was estimated according to Somerton's (1980) methodology. For this purpose, the following logistics model was adjusted by sexes: $Y = 1/1 + Ae^{BX}$, where *Y* is the adult ratio for the midpoint of a class interval (*X*), and A and B are undetermined parameters.

This estimation was performed by the particle swarm optimization algorithm (Kennedy & Eberhart 1995) by minimizing the objective function $\sum(Y\text{-}Y_{obs})^2$, where the Y_{obs} are the observed values of adult ratios by a class interval. The algorithm was restricted by the limits $1 \leq A \leq 30{,}000$ and $-1.0 \leq B \leq -0.3$ and by the minimum adult ratio (Y_{sar} = 0.021) at 10.5 cm TL. Y_{sar} = 2/FS, where F is the minimum fecundity (F = 9612 oocytes) at the smallest adult reported size of 10.5 cm TL for *M. curema* (Cabral-Solís et al. 2010) and S is the survival ratio (S = 0.01) of population individuals at the size of 10.5 cm TL. This estimation involves various assumptions: in size-zero, hatching generated the same number of larvae (~9612 = F); at 10.5 cm TL, 1% of the individuals survive (Dureuil & Froese 2021); assuming a sex ratio of 1:1, the number of individuals of each sex at 10.5 cm TL (*n*) is FS/2; if there is only one adult at 10.5 cm TL, the *Ysar* is 1/*n* or 2/FS. In addition, size at sexual maturity at other percentages (other than 50%) was estimated (L_{60}, L_{70}, L_{80}, L_{90}, and L_{95}) (Tsikliras et al. 2013).

RESULTS

Oogenesis stages

The earliest oogenesis stage observed was chromatin nucleolus oocytes, which were small in size *D* = 30.78 ± 43.07 µm (n = 1862), had a thin layer of basophil cytoplasm and had a comparatively large, less colored, very basophilic nucleolus at the center (Fig. 1a). The following stage was early perinucleolus oocyte *D* = 54.66 ± 45.3 µm (n = 2015), characterized by dense basophil cytoplasm and showed 4.5 ± 1.5 dispersed visible nucleoli in the nucleus periphery (Fig. 1b). Subsequently, late perinucleolar oocytes were developed, which were larger *D* = 77.18 ± 30.35 µm (n = 269) with a slightly less basophil cytoplasm than in the previous stage. The number of visible nucleoli in the nucleus periphery was larger (7 ± 1.2 nucleoli) (Fig. 1c). After that, the cortical alveoli oocyte was distinguished by showing lipid vacuoles in the cytoplasm (around the nucleus); the cytoplasm was less basophil, and the cell larger *D* = 99.35 ± 18.13 µm (n = 314) (Fig. 1d). The following stages were characterized by vitellogenesis occurrence. The vitellogenesis-1 oocyte showed yolk granules around the nucleus; the cytoplasm was acidophilic, and its diameter measured 161.2 ± 66.32 µm (n = 317) (Fig. 1e). The vitellogenesis-2 oocyte contained lipid vacuoles and yolk granules distributed in the cytoplasm (homogeneous appearance); the oocyte size was greater *D* = 309.17 ± 78.98 µm (n = 92) (Fig. 1f). The vitellogenesis-3 oocytes showed lipid vacuoles of greater size, and the oocyte diameter was 375.62 ± 44.29 µm (n = 273) (Fig. 1g). Final oocyte maturation occurred in the next stages. The migratory nucleus oocytes had a similar diameter *D* = 396.48 ± 95.34 µm (n = 43) regarding the previous stage. They were distinguished by presenting lipid droplets that come together in a single droplet in their most advanced state and whose fusion process may prolong until the next stage. The nucleus was found displaced toward the plasmatic membrane (animal pole), which lost its central position (Fig. 1h). The next oocyte stage was coalescence (C) *D* = 333.81 ± 18.13 µm (n = 314), where

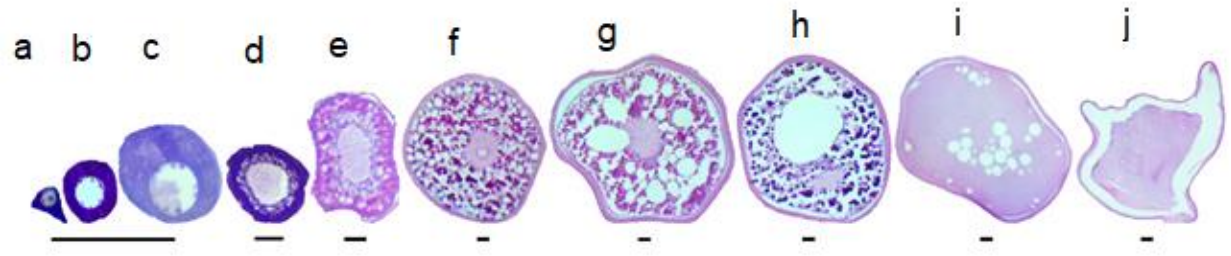

Figure 1. Oocyte stages of *Mugil curema*: a) chromatin nucleolus, b) early perinucleolar, c) late perinucleolar, d) cortical alveoli, e) vitellogenesis-1, f) vitellogenesis-2, g) vitellogenesis-3, h) migratory nucleus, i) coalescence, j) hydrated. The bar corresponds to a 100 µm. Hematoxylin-eosin stain.

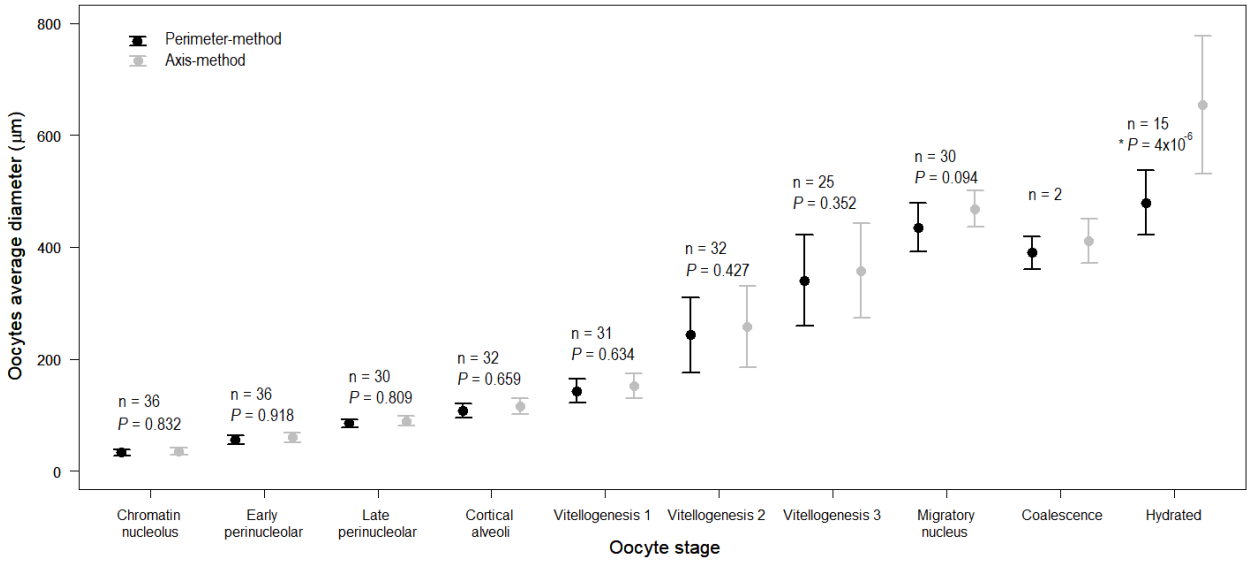

Figure 2. Average diameter of oocyte stages present in the different gonadal phases of *Mugil curema*. Black points show an estimation of the average diameter starting from the average of the greatest and lowest axes; gray points show average diameter estimation starting from the perimeter measurement; bars show standard deviation. *Statistical differences (Duncan's multiple range test, $P < 0.001$).

yolk granule coalescence occurred (Fig. 1i). Finally, the hydrated oocyte stage (Hy) was observed, where water accumulation and the oocyte diameter increased. However, when the oocytes were dehydrated during the histological technique, they showed an irregular shape with smaller dimensions $D = 479.5 \pm 77.7$ µm (n = 15). They were found free in the lumen wrapped only by the radiated zone (Fig. 1j). Kruskal-Wallis test showed an existing difference in diameters between axis-method and perimeter-method (Kruskal-Wallis test, $H_{19,528} = 509.34$; $P = 2.2 \times 10^{\wedge-16}$), and the *post-hoc* test showed differences in D measures of the Hy oocyte stage between methods (Fig. 2).

Gonad development

The reproductive system of *M. curema* has two gonadal lobules in ovaries and testicles fused in the posterior extreme, which also connects with the gonoduct ending in the genital pore. Each lobule has a main artery in a longitudinal position located in the proximal region and visible to the naked eye. As they develop, the testicles form a fold that hides the efferent duct and the main artery. *M. curema* gonads increase in size and change in color (light-intense yellow in ovaries; beige-white in testicles) as gamete production occurs, and their size is reduced when gametes are released.

The internal ovary structure is lamellar type, where oocytes are contained in conjunctive tissue extensions

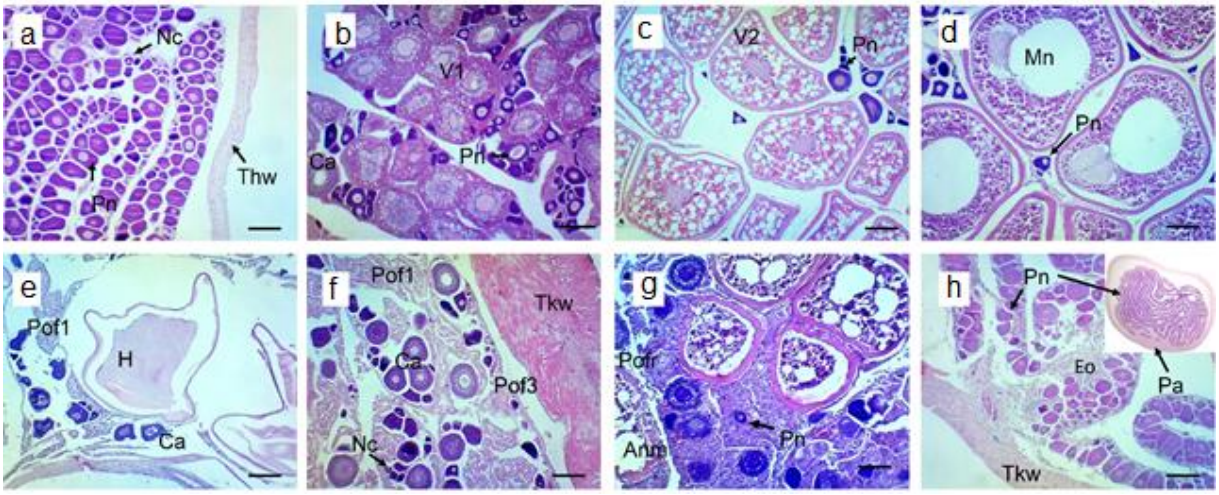

Figure 3. Ovarian phases of *Mugil curema*: a) immature, b) initial development, c) advanced development, d) mature, e) partial spawning, f) final spawning, g) reabsorption, h) rest (the box shows a panoramic image). Nc: chromatin nucleolus oocyte, Pn: perinucleolar oocyte, Ca: cortical alveoli, V1: vitellogenesis-1 oocyte, V2: vitellogenesis-2 oocyte, V3: vitellogenesis-3 oocyte, Mn: migratory nucleus oocytes, H: hydrated oocytes, Pof1: post-ovulatory follicles type one, Pof3: post-ovulatory follicles type three, Pofr: post-ovulatory follicles in reabsorption, Anm: atretic migratory nucleus oocytes, Thw: thin gonadal wall, Tkw: thick gonadal wall, Au: primary auricle. Eo: eosinophilic cells. Hematoxylin-eosin stain. Bar 100 µm.

(lamella) emerging from a narrow section of the proximal region in the gonadal lobule where the main artery is found (Fig. 3h). The testicles show an architecture in which the conjunctive tissue forms spermatic acini distributed in the organ. An efferent duct is found longitudinally in each testicular lobule, where spermatozoa accumulate to be ejected (Fig. 5a). Each gonad showed sexual cells of one sex only.

The ovarian development of *M. curema* was classified into six gonadal phases: immature, development (sub-phases: initial and advanced); mature, spawning (sub-phases: initial and final); reabsorption, and rest (Table 1, Fig. 3). The advanced development and maturity showed the simultaneous presence of oocytes in almost all the stages described in the same gonad (Fig. 4); whereas in the spawning phases, post-ovulatory follicles coexisted up to 2-3 different ages (Figs. 3e-f) and also oocytes in vitellogenesis (Fig. 3f) that remained after spawning. These observations indicate that the ovary development pattern is asynchronous, given the coexistence of three heterogeneous oocyte groups: previtellogenic, vitellogenesis, and maturity process (each with oocytes in different stages). Furthermore, a female could be capable of spawning from two to three oocyte batches in a brief period of days, that is, a partial spawning, and the ovaries could be capable of reinitiating the development starting from a heterogeneous group of oocytes in vitellogenesis that remain after spawning.

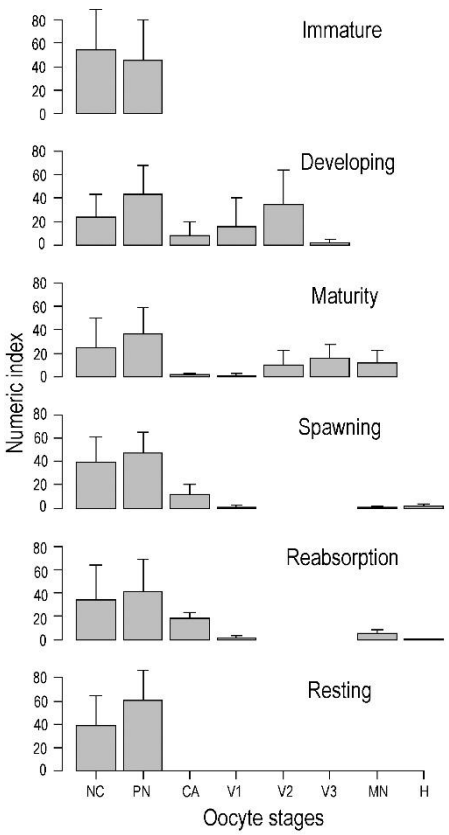

Figure 4. Numerical index average for each oocyte stage and each gonadal phase of *Mugil curema*. The bar shows the standard deviation.

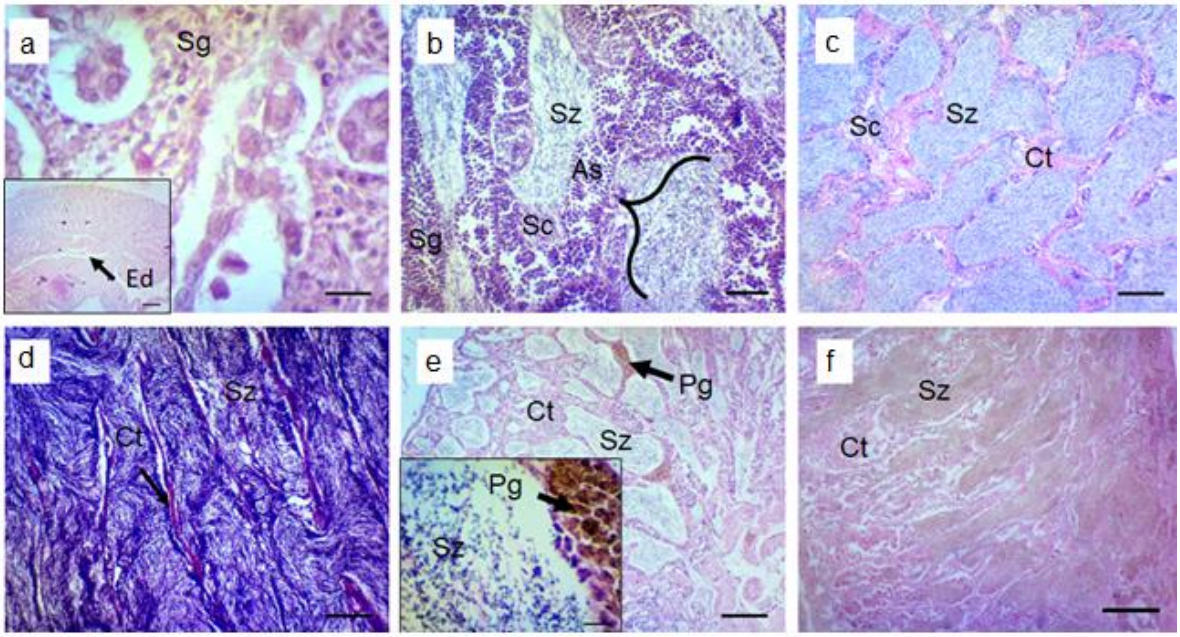

Figure 5. Testicular phases of Mugil curema: a) immature (the box shows a panoramic image; large bar 10 µm, small bar 100 µm); b) development; c) initial ejaculation; d) final ejaculation; e) reabsorption (small bar 10 µm, large bar 100 µm); f) rest. Sg: spermatogonia, Sc: spermatocytes, Sz: spermatozoids, As: acini, Ct: conjunctive tissue, Pg: phagocytes, Ed: efferent duct. Hematoxylin-eosin stain. The bar indicates 100 µm in the figures b, c, d and f.

The testicular development were classified in five phases and two gonadal sub-phases: immature, development, ejaculation (initial and final), reabsorption, and rest (Table 2, Fig. 5). Additionally, spermatogenesis of *M. curema* is asynchronous since it was possible to observe different stages of the male cells simultaneously in development (spermatocytes and spermatids) in the spermatic acinus. Furthermore, spermatogenesis and spermiogenesis were shown continuously during the development phases and initial ejaculation, so the spermatozoids accumulated in the acinus lumen of the spermatic and efferent duct and continued producing even when the testicle was ejaculating.

Sex-ratio

In total, 626 organisms were analyzed, of which 352 were females and 274 males. The sex ratio of the total sample was 0.77 males per one female (chi-square test, $\chi^2 = 9.71$, $P = 0.002$), observing bias toward a greater number of females in the population. Sex ratio by size interval showed a succession in sex dominance as size increased. The sample was composed of only males in smaller sizes, and females were recorded from the size class of 20.5 cm in TL (midpoint). Female proportion and frequency started an increasing tendency toward larger sizes as male presence reduced (Fig. 6). Larger males were represented until 32.5 cm in TL size class, and in larger sizes than this one, only females were recorded. Sex ratio 1:1 was observed only in 24.5 and 25.5 cm in TL size class ($\chi^2 = 0.473$, $P = 0.491$ and $\chi^2 = 0.13$, = 0.718, respectively) (Fig. 6).

Sexual maturity

Size structures of females against males were statistically different (Dmax = 0.499, $P = 2.21\times10^{-16}$), for which sexual maturity sizes were estimated separately (Fig. 7). Size at sexual maturity (L_{50}) for females was 22.08 cm and for males 18.26 cm, according to optimal parameters A = 1519.35 and B = -0.33 for females and A = 8628.89 and B = -0.50 for males. Figure 7 shows other estimations of size at sexual maturity.

DISCUSSION

Oocyte stages of *Mugil curema* follow the general development pattern for bony fish: primary growth, chromatin nucleolus (CN) and perinucleolar oocyte (PN) (early and late); yolk vesicle formation, cortical alveoli (CA); true vitellogenesis, V1, V2, and V3; and maturity, migratory nucleus oocytes (MN), C, and Hy (Wallace & Selman 1981, DeVlaming et al. 1982, Greeley et al. 1987), showing similar characteristics to those described by Solomon & Ramnarine (2007) in *M. curema* of the Gulf of Paria, Trinidad. The oocyte

Table 1. Histological description of the gonadal development of females of *Mugil curema*

Phase	Description
Immature	Chromatin nucleolus oocyte (CN), numerical index (*NI*) = 54.5 ± 34 and perinucleolar oocyte (PN, *NI* = 45.5 ± 34) were observed. The distribution of the cells is compact. Eosinophilic cells showed between the connective and germinal tissue, and the ovarian wall is thin, 39.6 ± 5.9 µm (n = 38). *D* of the oocytes was 46.4 ± 6 µm (n = 1122) (all stages) and the gonadosomatic index (*GSI*) = 0.5 ± 0.65 (n = 70) (Figs. 2, 3a, 4). Highlights stromal elongation that was observed like lamella formation in all samples.
Development	Some oocyte cohorts were found in secondary growth (vitellogenesis). The CN and PN oocytes continue present with a *NI* of 23.3 ± 20 and 43.5 ± 24, respectively. Sub-phases a) initial development: besides the CN and PN, cortical alveoli oocytes are present (CA, *NI* = 13.3 ± 16.06); *D* of the oocytes was 61.4 ± 10.7 µm (n = 1526) (all stages) and *GSI* = 0.92 ± 0.66 (n = 83) (Figs. 2, 3b, 4).
Advanced development	Presence of CN and PN, and also vitellogenesis-1 (V1, *NI* = 15.4 ± 24.7), vitellogenesis-2 (V2, *NI* = 34 ± 30) and vitellogenesis-3 (V3, *NI* = 2 ± 3) oocytes; *D* of the oocytes was 62.03 ± 11.5 µm (n = 1073) (all stages) and *GSI* = 3.9 ± 3.1 (n = 96) (Figs. 2, 3c, 4).
Mature	Oocytes in vitellogenesis (V1, V2, V3; *NI* = 26.2 ± 26.2) and in maturity (migratory nucleus oocytes, MN; *NI* = 11.4 ± 11.7) dominate; *D* of the oocytes was 199.3 ± 73.3 µm (n = 534) (all stages) and the *GSI* = 9.06 ± 4.4 (n = 96) (Figs. 2, 3d, 4). The CN and PN were also present (*NI* = 24.9 ± 25 and 35.8 ± 23.1, respectively).
Spawning	Characterized by the presence of post-ovulatory follicles (POF), which indicated the recent occurrence of oocytes ejection. The POF up to three different ages may simultaneously be present. Sub-phases a) partial spawning: besides the POF, the presence of oocytes NM or Hy (*NI* = 1.05 ± 0.5; 1.5 ± 2.5, respectively) were observed; *D* of the oocytes was 109.4 ± 73.1 µm (n = 193) (all stages) and the *GSI* = 4.1 ± 6 (n = 14) (Figs. 2, 3e, 4).
Final spawning	Characterized by the presence of a great POF proportion, the average *D* of the oocytes was 69 ± 3.7 µm (n = 346) and *GSI* = 1.7 ± 1.4 (n = 27). In both sub-phases, CN, PN, CA and V1 oocytes (*NI* = 39.3 ± 21.1; 46.7 ± 18; 11.6 ± 14.07; 0.9 ± 0.2, respectively) may be observed (Figs. 2, 3f, 4).
Reabsorption	Characterized by the presence of oocyte atresia NM and Hy (*NI* = 5.1 ± 3, 0.46 ± 0.4, respectively), as well as POF in advanced reabsorption stage; *D* of the oocytes was 50.4 ± 7.6 µm (n =219) (all stages) and *GSI* = 1.1 ± 0.5 (n = 5). Additionally, CN, PN, CA and V1 oocytes (*NI* = 33.6 ± 30, 40 ± 28, 18.4 ± 4, 1.5 ± 1.5, respectively) are observed (Figs. 2, 3g, 4).
Rest	The CN and PN (*NI* = 39 ± 25, 60 ± 25) oocytes are present; the conjunctive tissue of the stroma had a thickened appearance, between the connective and germinal tissue showed eosinophilic cells, and the ovarian wall was three times thicker (120 ± 23 µm; n = 25) than in the immature phase; *D* of the oocytes was 46 ± 7.1 µm (n =771) (all stages) and *GSI* = 0.98 ± 1.5 (n = 39) (Figs. 2, 3h, 4).

diameter of CN, PN, and CA of *M. curema* in the coastal lagoon Barra de Navidad, Jalisco, Mexico (Ruiz-Ramírez et al. 2017) and in the Gulf of Paria, Trinidad (Solomon & Ramnarine 2007) were similar to those observed in this research. In contrast, starting from the vitellogenesis stages, differences were observed. These differences suggest that oocytes of *M. curema* that inhabit latitudes ~19°N (Barra de Navidad lagoon) and ~10.2°S (Gulf of Paria) reached a smaller average size (MN stage, *D* was 269 and 227-412 µm, respectively) concerning oocytes south of Sinaloa at ~23°N (MN, *D* = 435.34 µm). Bergman's rule could explain this latitudinal variation, which has suggested alternative mechanisms for latitudinal size clines driven by primary productivity, heat load, and environmental predictability (Meiri 2011). The trend in fish towards tropical zones to present a longer spawning season (Cushing 1975) could be part of mechanisms that limit the size of the oocytes as a result of energy investment to support a greater number of spawning compared to colder latitudes. C oocytes were not observed in the Gulf of Paria (Solomon & Ramnarine 2007), possibly due to the brevity of occurrence. Given that the samplings in this study were more frequent (weekly), a greater possibility of finding them existed.

The *D* measurements of Hy oocyte made from the axis method showed bias due to oocyte dehydration and deformation on account of the histological technique. So the *D* values of Hy were lower than in the previous stages (NM or C) when they should have been greater. For this reason, some authors (e.g. Solomon & Ramnarine 2007, Ruiz-Ramírez et al. 2017) could have omitted measurements from the axis method. An alternative could be the perimeter method in which the deformity of the oocyte due to dehydration does not affect because the perimeter from deformed structures can be measured precisely. Then *D* is calculated using an arithmetic equation, assuming that the structure is a circle. In this case (*M. curema*), the *D* of Hy stage oocytes were greater from the perimeter method, and

Table 2. Histological description of the gonadal development of males of *Mugil curema*.

Immature	The appearance of the conjunctive tissue of the testicular stroma was compact, and the acinus lumen was not completely defined. Presence of spermatogonia and spermatocytes is observed in the acini walls. Thickness of the testicle wall was 7.76 ± 3.4 µm (n =38) and gonadosomatic index (*GSI*) = 0.5 ± 0.81 (n = 38) (Fig. 5a).
Development	The acinus shape was well-defined and showed spermatozoids in the lumen. Moreover, the acinus wall was thickened by spermatozoids and spermatids proliferation, and spermatogonia were also present. *GSI* = 1.92 ± 1.55 (n = 87) (Fig. 5b).
Initial ejaculation	A great number of spermatozoids were contained in the efferent duct, and ejaculation occurrence is evidenced by spermatozoid density reduction and acini narrowing. The acini and efferent duct were full of spermatozoids, and their walls were stretched (thin appearance) with the presence of spermatogonia and proliferation of spermatocytes and spermatids. *GSI* = 2.6 ± 2.3 (n = 41) (Fig. 5c).
Final ejaculation	The presence of germinal cells was almost null, evidencing that spermatogenesis had ended, whereas acini and the efferent duct were still full of spermatozoids with their walls stretched. *GSI* = 2.68 ± 3.01 (n = 83) (Fig. 5d).
Reabsorption	The conjunctive tissue of the stroma was thick; spermatogonia and phagocytes were observed in acini besides other remnants, both in the lumen and the walls. *GSI* = 1.55 ± 0.92 (n = 9). This phase was little observed, indicating that the process occurred rapidly.
Rest	The stroma conjunctive tissue was thick and elongated, without germinal cells and possible spermatozoid remnants in the efferent duct; testicle wall thickness was 19 ± 4.12 µm (n = 11) (Figs. 5e-f). *GSI* = 1.49 ± 1.2 (n = 11).

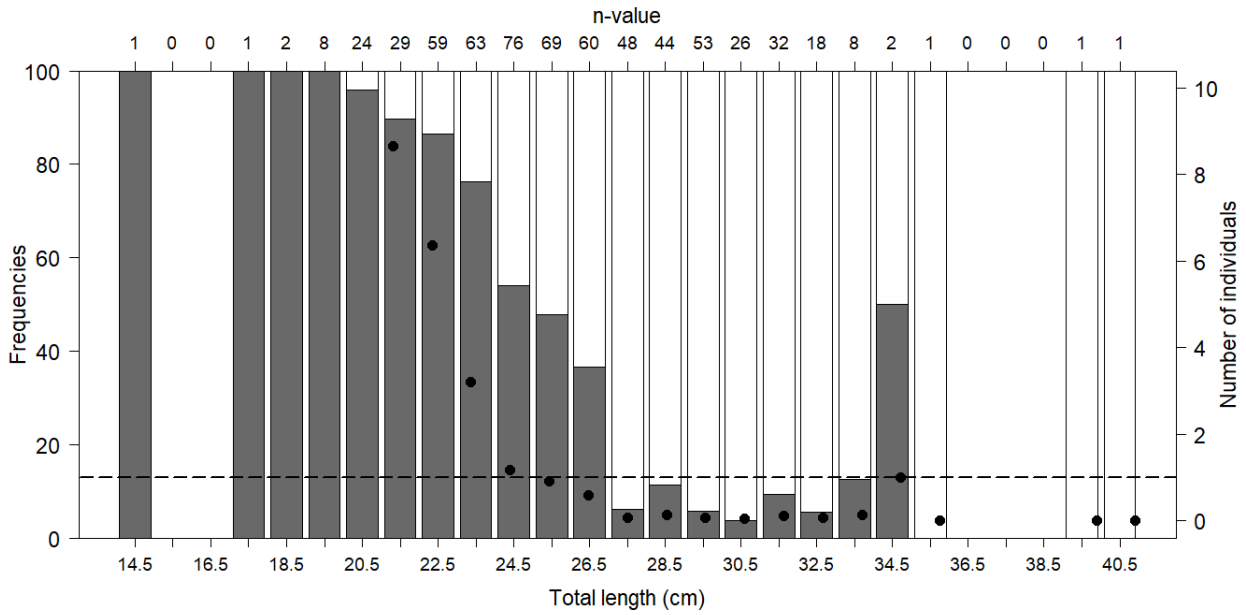

Figure 6. *Mugil curema* sex composition structure by size represented through frequencies of males (gray bars) and females (white bars) by the midpoint of class size and the number of males (black circle) for each female (dotted line) by size.

these estimations were very close (429 to 875 µm, 654.4 µm on average) to the diameter of the eggs measured in culture (770 to 920 µm, Anderson 1957). The observations suggest that a closer estimation of *D* between histological slides and fresh oocytes and eggs is possible with the perimeter method. So the perimeter method is recommended as a better alternative method to measure diameters from histological slides in oocytes with spherical form.

The *M. curema* ovaries show an asynchronous development pattern since almost all the oocyte stages are observed in the same gonad in the advanced and mature phases (Marza 1938, Wallace & Selman 1981). Therefore, the coexistence of three heterogeneous oocyte groups (previtellogenesis, vitellogenesis, and maturity) may be identified. On the other hand, Greeley et al. (1987) demonstrated that *Mugil cephalus* has a group-synchronous type of oogenesis characterized by

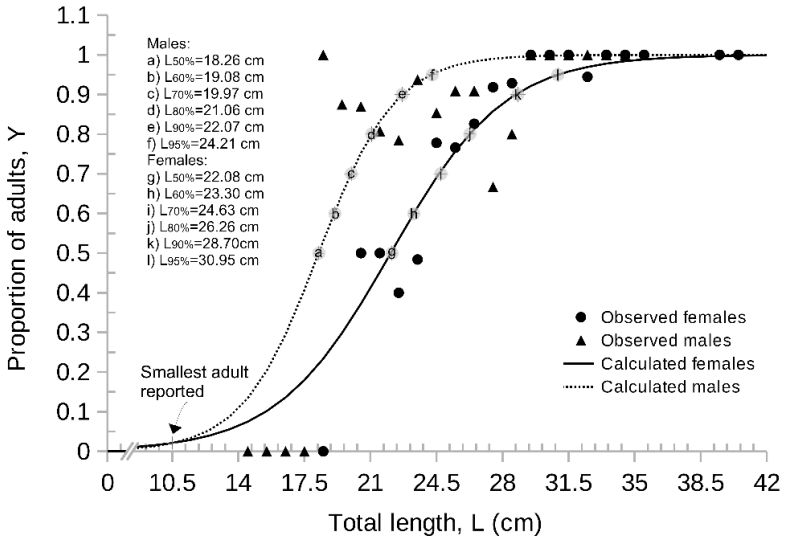

Figure 7. Proportions of adult females and males of *Mugil curema*. Continuous and dotted lines show optimized models for females and males, respectively. a-l) Sizes at sexual maturity corresponding to a percentage of adults.

the coexistence of a single developing clutch of oocytes and a pool of previtellogenic oocytes. This result suggests that one female of *M. cephalus* spawns only once a year because no more than a single clutch of developing oocytes has ever been observed proceeding through vitellogenesis during the fall period of pre-spawning ovarian recrudescence (Greeley et al. 1987). Whereas a female of *M. curema* can spawn more than once a year, since a heterogeneous group of oocytes in vitellogenesis stages remains after spawning, the ovaries may restart development.

Moreover, *M. curema* has also been defined as a batch spawner since it spawns different batches of oocytes in days, evidenced by the simultaneous post-ovulatory follicles (POF) presence of different ages, indicating the previous close spawns (Ganias et al. 2014). Besides POF, vitellogenic (V3) and oocytes in maturity (NM and Hy) were also observed during the actively spawning phase, suggesting that another batch of oocytes would be released shortly (Brown-Peterson et al. 2011). This spawning pattern of *M. curema* was also defined in the Gulf of Paria (Solomon & Ramnarine 2007). The ovary type development definition in *M. curema* contrasts with observations in other areas, where it was defined as group-synchronous (Solomon & Ramnarine 2007, Albieri et al. 2010a,b, Rocha de Oliveira et al. 2011, Fernandez & Dias 2013, Ruiz-Ramírez et al. 2017, Salgado-Cruz 2020). In line with Greeley et al. (1987), this study recommends the oocyte size-frequency profile method applied by these authors or the modified method applied here, plus the additional histological evidence to define the type of ovarian development pattern.

The ovarian development of *M. curema* was classified into six gonadal phases: immature, development (sub-phases: initial and advanced); mature, spawning (sub-phases: initial and final); reabsorption, and rest. Despite different nomenclature, these ovarian phases were similar in number and the processes described in Sepetiba Bay, Rio de Janeiro, Brazil (Albieri 2009, Albieri et al. 2010a,b). Whereas other works, only up to four ovarian phases were identified (Rocha de Oliveira et al. 2011, Fernandez & Dias 2013, Salgado-Cruz 2020).

Testicular development of *M. curema* was classified into five phases: immature, development, ejaculation (sub-phases: initial and final), reabsorption, and rest. Salgado-Cruz (2020) described only three of the phases observed in this study (immature, development, and ejaculation), but they distinguished two sub-phases of development (early and late). Such a study did not observe the reabsorption and rest phases, possibly because these phases could be brief since they were rarely observed in this study. Despite the differences among phase classifications, the converging aspects among the different studies are similar. However, and in contribution to knowledge, this study provides more detailed qualitative and quantitative descriptions. For example, integrating the numerical index (*NI*) of each oocyte stage helps to understand the ovarian phases better since it provides data on the percentage of each

oocyte stage in histological sections, so its use is recommended.

Sex ratio by size intervals showed a succession in sex dominance as size increased, such that in smaller sizes, only males were recorded (<20.5 cm TL) and only females in larger sizes (>34.5 cm TL), with a 1:1 sex ratio only in size classes of 24.5 and 25.5 cm TL. This sex composition structure by size in *M. curema* is characteristic of protandrous species (Sadovy & Shapiro 1987). Ibáñez-Aguirre et al. (2006) observed that in the Atlantic and the Pacific oceans, the average size in females was longer (27 cm) than in males (25 cm). Franco de Olivera et al. (2011) also observed only males in sizes smaller than 15 cm TL and female dominance in sizes greater than 33 cm TL in the Potengi River estuary, Brazil. Subsequently, Ruiz-Ramírez et al. (2017) documented a similar sex composition structure by size in the Barra de Navidad Lagoon, Jalisco, Mexico. Salgado-Cruz (2020, 2021) in two fishing sites on the coast of Baja California Sur showed that the major frequency of males was 29.5 to 30.5 cm in Bahia de La Paz and 31.5 to 32.5 cm in Bahia Magdalena and the major frequency of female was 31.5 to 33.5 and 33.5 to 34.5 cm respectively. Also, other background suggests it deals with a gonochoristic species (Chávez-Herrera 1993, González-Castro & Minos 2015). This study could not identify testicular components or vestigial male germinal tissue in ovaries, a common condition that occurs in fully transformed ovaries of protandrous species with undelimited gonadal tissue (Sadovy & Shapiro 1987). However, using structural features, protandrous species are difficult to identify (Sadovy & Shapiro 1987). The internal structure of *M. curema* ovaries is notably similar to the resulting ovarian structure starting from the feminization of *Oreochromis mossambicus* (=*Tilapia mossambica*) genetic males with estrogen treatment. Stromal elongation (lamella formation) was observed from the proximal region of affected testes (Nakamura 2013). Furthermore, eosinophilic cells were observed in the ovarian stroma of *M. curema*, whose prevalence in intersexual individuals of the sequential hermaphrodite *Coris julis* could indicate a relationship between that cell type and sex change process (Alonso-Fernández et al. 2011). The eosinophilic cells are also present during the testicular involution stage of the protandrous hermaphroditic species *Sparus aurata* (Liarte et al. 2007). The observations in this study could lay the foundations for future research to show that *M. curema* could be protandrous hermaphroditic species.

The onset of sexual maturity is a biological threshold of a species' life cycle that marks the transition in which a juvenile (sexually immature) passes to be an adult (sexually mature; capable of reproducing), and its occurrence is closely related to size (Policansky 1983). Usually, the size at sexual maturity in fish is estimated by the length at which 50% of the population becomes mature for the first time (Somerton 1980). However, it may also be estimated at other percentages than 50% (Tsikliras et al. 2013), generally assuming a percentage because not all individuals in the population start sexual maturity at the same size. For its estimation, the ratio of adult organisms should be represented concerning juveniles in each class size (Somerton 1980). The total size interval should cover the sizes where the smallest adult is present. In this study, the sample structure was mainly affected out of the catch area by the smallest individual distribution. Thus, the adult ratio observed concerning juveniles smaller than ~19 cm TL was poorly represented, starting from 0.50 in females (50% adults) to 0.88 in males (80% adults). Therefore, the logistics model for estimating L_{50} was adjusted, assuming a minimum adult ratio of 0.021 starting from the size of the smallest adult reported by Cabral-Solís et al. (2010; 10.5 cm TL). According to the data, this adjustment helped make a good adjustment to the logistics function. It also granted biological consistency to adjust the tendency in smaller sizes, strengthening the estimation of sizes at sexual maturity starting from L_{50}. Therefore, this method could mitigate bias that adds to the L_{50} estimation when the sample is affected in smaller sizes, which is generally caused by the selectivity of fishing gear. Nonetheless, it is difficult to define when sexual maturity variation is due to biological and ecological factors in comparative works.

In this study, L_{50} estimated for males was 18.26 cm TL and for females, 22.08 cm TL. In general, males of *M. curema* have been reported to have smaller L_{50} than females in different areas, such as, Tamiahua Lagoon, Mexico (Ibañez-Aguirre & Gallardo-Cabello 2004), Barra de Navidad Lagoon, Mexico (Ruiz-Ramírez et al. 2017), La Paz Bay and Magdalena Bay, Mexico (Salgado-Cruz 2020, Salgado-Cruz et al. 2020), which is related with bias size structure of males in small sizes (Trippel & Harvey 1991). Contrastingly, Cabral-Solís et al. (2010) and Franco de Oliveira et al. (2011) estimated L_{50} larger in males than in females in Cuyutlán Lagoon, Mexico, and Potengi River estuary, Brazil, respectively, and none reported size segregation by sex. In other works, a difference between sexes was not possible to observe since they reported L_{50} population or only for females in Brazil coast (Rocha de Oliveira et al. 2011); Venezuela coast (Marín & Dodson 2000); Michoacán coast (Meléndez-Galicia & Romero-Acosta 2020).

This information is greatly relevant for fishery management since it could support a possible modi-

fication of the legal catch size in the southeast of the Gulf of California, as well as readjusting the production models of the stock under the premise that it is a partial spawner with gonadal asynchronous development. In addition, the management plans of world fisheries could incorporate precautionary management measures to minimize the risks of overexploitation. At the same time, no *M. curema* sexuality is defined because of the possibility that this specie could be protandrous hermaphrodite and due to the vulnerability associated with these biological attributes in fisheries (Provost & Jensen 2015).

ACKNOWLEDGMENTS

The authors are grateful to PRODEP "Forzamiento ambiental en especies clave de los ecosistemas acuáticos" (Convenio DSA 511-6/17-7679 Folio UAS-PTC-131), as well as to Consejo Nacional de Ciencia y Tecnología (CONACYT), Mexico for their support through the graduate stay program Estancia Post-doctoral por México en la modalidad Académica (Application number 60128) and Sistema Nacional de Investigadores (SNI); to Diana Fischer for translation and edition.

REFERENCES

Albieri, R.J. 2009. Biologia reproductiva da Tainha *Mugil liza* Valenciennes e do Parati *Mugil curema* Valenciennes (Actonopterygii, Mugilidae) na Baia de Sepetiba, RJ, Brasil. Tesis Maestría en Ciencias, Universidad Federal Rural do Rio de Janeiro, Rio de Janeiro.

Albieri, R.J., Araújo, F.G. & Ribeiro, T.P. 2010a. Gonadal development and spawning season of white mullet *Mugil curema* (Mugilidae) in a Tropical Bay. Journal of Applied Ichthyology, 26: 105-109. doi: 10.1111/j.1439-0426.2009.01369.x

Albieri, R.J., Araújo, F.G. & Uehara, W. 2010b. Differences in reproductive strategies between two co-occurring mullets *Mugil curema* Valenciennes 1836 and *Mugil liza* Valenciennes 1836 (Mugilidae) in a Tropical Bay. Tropical Zoology, 23: 51-62.

Alonso-Fernández, A., Alós, J., Grau, A., Domínguez-Petit, R. & Saborido-Rey, F. 2011. The use of histological techniques to study the reproductive biology of the hermaphroditic Mediterranean fishes *Coris julis*, *Serranus scriba*, and *Diplodus annularis*. Marine and Coastal Fisheries, 3: 145-159. doi: 10.1080/19425120.2011.556927

Anderson, W.W. 1957. Early development, spawning, growth, and occurrence of the silver mullet (*Mugil curema*) along the South Atlantic coast of the United States. Fishery Bulletin, 119: 397-414.

Baumar, J.E.M. & Dodson, J.J. 2000. Age, growth and fecundity of the silver mullet, *Mugil curema* (Pisces: Mugilidae), in coastal areas of northeastern Venezuela. Revista de Biología Tropical, 48: 1-14. doi: 10.15517/RBT.V48I2-3.18755

Blaber, S.J.M. 1997. Fish and fisheries of tropical estuaries. Chapman & Hall, London.

Briones-Ávila, E. 1998. Biología y pesquería de *Mugil cephalus* en la Laguna de Agua Brava, Nayarit, durante 1992-1994. Master's Thesis, Universidad Autónoma de Sinaloa, Sinaloa.

Brown-Peterson, N.J., Wyanski, D.M., Saborio-Reyes, F., Macewicz, B.J. & Lowerre-Barbieri, S.K. 2011. A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries, 3: 52-70. doi: 10.1080/19425120.2011.555724

Cabral-Solís, E.G., Gallardo-Cabello, M., Espino-Barr, E. & Ibáñez, A.L. 2010. Reproduction of *Mugil curema* (Pisces: Mugilidae) from the Cuyutlán Lagoon, in the Pacific Coast of México. Avances en Investigación Agropecuaria, 14: 19-32.

Castro-Aguirre, J.L. 1978. Catálogo sistemático de los peces marinos que penetran a las aguas continentales de México con aspectos zoogeográficos y ecológicos. Instituto Nacional De Pesca, Serie Científica 19. [https://agris.fao.org/agris-search/search.do?recordID=XF2015008067]. Reviewed: June 11, 2021.

Chávez-Herrera, D. 1993. Aspectos biológicos de *Mugil curema* Cuvier Valenciennes, *Mugil cephalus* Lineo y *Mugil hospes* Jordan y Culver; en dos lagunas costeras del sur de Sinaloa. Bachelor's Thesis, Instituto Politécnico Nacional, Ciudad de México.

Cushing, D.H. 1975. Ecología marina y pesquerías. Editorial Acribia, Zaragoza.

DeVlaming, V., Grossman, G. & Chapman, F. 1982. On the use of the gonosomatic index. Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology, 73: 31-39. doi: 10.1016/0300-9629(82)90088-3

Durand, J.D., Shen, K.N., Chen, W.J., Jamandre, B.W., Blel, H., Diop, K., et al. 2012. Systematics of the grey mullet (Teleostei: Mugiliformes: Mugilidae): molecular phylogenetic evidence challenges two centuries of morphology-based taxonomic studies. Molecular Phylogenetics and Evolution, 64: 73-92. doi: 10.1016/j.ympev.2012.03.0006

Dureuil, M. & Froese, R. 2021. A natural constant predicts survival to maximum age. Communications Biology, 641: 1-6. doi: 10.1038/s42003-021-02172-4

Fernandez, W.S. & Dias, J.F. 2013. Aspects of the reproduction of *Mugil curema* (Valenciennes, 1836) in two coastal systems in southeastern Brazil. Tropical

Zoology, 26: 15-32. doi: 10.1080/03946975.2013.775052

Franco de Oliveira, M., Dos Santos, C.E.F., De Morais, F.F.A., Lins, D.J.E. & Luchiari, A.C. 2011. Some aspects of the biology of white mullet, *Mugil curema* (Osteichthyes, Mugilidae), in the northeastern region of Brazil. Pan-American Journal of Aquatic Sciences, 6: 138-147.

Ganias, K., Murua, H., Claramunt, G., Domínguez-Petit, R., Gonçalves, P., Juanes, F., et al. 2014. Egg production. In: Domínguez-Petit, R., Murua, H., Saborido-Rey, F. & Trippel, E. (Eds.). Handbook of applied fisheries reproductive biology for stock assessment and management, Digital CSIC, Vigo.

González-Castro, M. & Minos, G. 2015. Sexuality and reproduction of Mugilidae. In: Crosetti, D. & Blaber, S. (Eds.). Biology, ecology and culture of grey mullet (Mugilidae). CRC Press, Boca Raton.

Greeley Jr., M.S., Calder, D.R. & Wallace, R.A. 1987. Oocyte growth and development in the striped mullet, *Mugil cephalus*, during seasonal ovarian recrudescence: relationship to fecundity and size at maturity. Fishery Bulletin, 85: 187-200.

Humason, L.G. 1979. Animal tissue techniques. W.H. Freeman, San Francisco.

Ibáñez-Aguirre, A.L. & Colín, A. 2014. Reproductive biology of *Mugil curema* and *Mugil cephalus* from western Gulf of Mexico waters. Bulletin of Marine Science, 90: 941-952. doi: 10.5343/bms.2014.1004

Ibáñez-Aguirre, A.L. & Gallardo-Cabello, M. 2004. Reproduction of *Mugil cephalus* and *M. curema* (Pisces: Mugilidae) from a coastal lagoon in the Gulf of Mexico. Bulletin of Marine Science, 75: 37-49.

Ibáñez-Aguirre, A.L., Cabral-Solís, E., Gallardo-Cabello, M. & Espinosa-Barr, E. 2006. Comparative morphometrics of two populations of *Mugil curema* (Pisces: Mugilidae) on the Atlantic and Mexican Pacific coasts. Scientia Marina. 70: 139-145.

Kennedy, J. & Eberhart, R. 1995. Particle swarm optimization. Proceedings of the IEEE International Conference on Neural Networks, 4: 1942-1948. doi: https://doi.org/10.1109/ICNN.1995.488968

Liarte, S., Chaves-Pozo, E., García-Alcazar, A., Murelo, V., Meseguer, J. & García-Ayala, A. 2007. Testicular involution prior to sex change in gilthead seabream is characterized by a decrease in DMRT1 gene expression and by massive leukocyte infiltration. Reproductive Biology and Endocrinology, 5: 20. doi: 10.1186/1477-7827-5-20

Lowerre-Barbieri, S.K., Brown-Peterson, N.J., Murua, H., Tomkiewicz, J., Wyanski, D.M. & Saborido-Rey, F. 2011. Emerging issues and methodological advances in fisheries reproductive biology. Marine and Coastal Fisheries, 3: 32-51. doi: 10.1080/19425120.2011.555725

Lucano-Ramírez, G. 1991. Estudio sobre madurez gonádica y estructura poblacional de *Mugil curema* Valenciennes 1836 (Lisa) en la laguna costera Agua Dulce, Jalisco, México. Tesis Profesional, Universidad de Guadalajara, Guadalajara.

Lucano-Ramírez, G. & Michel-Morfin, J.E. 1997. Ciclo reproductivo y aspectos poblacionales de *Mugil curema* Valenciennes, 1836 (Pisces: Mugilidae) en la laguna costera Agua Dulce, Jalisco, México. Oceanologia, 1: 105-115.

Marin, B.J. & Dodson, J.J. 2000. Age, growth and fecundity of the silver mullet, *Mugil curema* (Pisces: Mugilidae), in coastal areas of northeastern Venezuela. International Journal of Tropical Biology and Conservation, 48: 389-398. doi: 10.15517/RBT.V48I2-3.18755.

Marin, B.J., Quintero, A., Bussiere, D. & Dodson, J.J. 2003. Reproduction and recruitment of white mullet (*Mugil curema)* to a tropical lagoon (Margarita Island, Venezuela) as revealed by otolith microstructure. Fishery Bulletin, 101: 809-821.

Maldonado-Amparo, M.A., Sánchez-Cárdenas, R., Salcido-Guevara, L.A. & Ramírez-Pérez, J.S. 2017. Gonadal development of *Peprilus medius* (Peters, 1869) (Perciformes: Stromateidae) from southeast of the Gulf of California, Mexico. International Journal of Morphology, 35: 56-61. doi: https://doi.org/10.4067/S0717-95022017000100011

Marza, V.D. 1938. Histophysiology of oogenesis. Hermann and Co., London.

Meiri, S. 2011. Bergmann's rule-What's in a name? Global Ecology and Biogeography, 20: 203-207. doi: https://doi.org/10.1111/j.1466-8238.2010.00577.x

Meléndez-Galicia, C. & Romero-Acosta, A.C. 2010. Evaluación biológico pesquera de la lisa *Mugil curema*, en la costa de Michoacán. Ciencia Pesquera, 18: 67-77.

Nakamura, M. 2013. Morphological and physiological studies on gonadal sex differentiation in teleost fish. Aqua-BioScience Monographs, 6: 1-47. doi: 10.5047/absm.2013.00601.0001

Parenti, L.R. & Grier, H.J. 2004. Evolution and phylogeny of gonad morphology in bony fishes. Integrative and Comparative Biology, 44: 333-348. doi: 10.1093/icb/44.5.333

Pianka, E.R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics, 4: 53-74. doi: 10.1146/annurev.es.04.110173.000413

Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. American Zoologist, 23: 57-63. doi: 10.1093/icb/23.1.57

Provost, M.M. & Jensen, O.P. 2015. The impacts of fishing on hermaphoditic and treatment of sex change in stock assessments. Fisheries, 40: 536-545. doi: https://doi.org/10.1080/03632415.2015.1093471

Robins, C.R., Bailey, R.M., Bond, C.E., Brooker, J.R., Lachne, E.A., Lea, R.N. & Scott, W.B. 1991. Common and scientific names of fishes from the United States and Canada. American Fisheries Society, Bethesda.

Rocha de Oliveira, M., Dos Santos Costa, E.F. & Chellappa, S. 2011. Ovarian development and reproductive period of white mullet, *Mugil curema* in the coastal waters of northeastern Brazil. Animal Biology Journal, 2: 199-212.

Ruiz-Ramírez, S., Molina-Arenas, E.G., Lucano-Ramírez, G., Aguilar-Betancourt, C., Flores-Ortega, J.R., Kosonoy-Aceves, D. & González-Sansón, G. 2017. Aspectos reproductivos de la lisa *Mugil curema* (Mugiliformes: Mugilidae) en la laguna costera de Barra de Navidad, Jalisco, México. Latin American Journal of Aquatic Research, 45: 443-456.

Sadovy, Y. & Shapiro, D.Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia, 1987: 136-156. doi: 10.2307/1446046

Salgado-Cruz, L. 2020. Estrategia reproductiva vinculada a la edad y al crecimiento de la lisa rayada *Mugil cephalus* Linnaeus, 1758 y de la liseta *Mugil curema* Valenciennes, 1836 en dos zonas de Baja California Sur, México. Ph.D. Thesis, Instituto Politécnico Nacional, Ciudad de México.

Salgado-Cruz, L., Quiñonez-Velázquez, C., García-Domínguez, F.A. & Pérez-Quiñonez, C.I. 2020. Detecting *Mugil curema* (Perciformes: Mugilidae) phenotypic stock in La Paz Bay, Baja California Sur, Mexico, using geometric morphometrics of otolith shape, growth, and reproductive parameters. Revista Mexicana de Biodiversidad, 91: e913273. doi: 10.2220/ib.200787706e.2020.91.3273

Salgado-Cruz, L., Quiñonez-Velázquez, C. García-Domínguez, F.A., Pérez-Quiñonez, C.I. & Aguilar-Camacho, V. 2021. Aspectos reproductivos de *Mugil curema* (Perciformes: Mugilidae) en dos zonas de Baja California Sur, México. Revista de Biología Marina y Oceanografía, 56: 50-65. doi: 10.22370/rbmo.2021.56.1.2798

Received: September 8, 2021; Accepted: May 4, 2022

Schulz, R.W., De França, L.R., Lareyre, J.J., LeGac, F., Chiarini-Garcia, H., Nobrega, R.H. & Miura, T. 2010. Spermatogenesis in fish. General and Comparative Endocrinology, 165: 390-411. doi: 10.1016/j.ygcen.2009.02.013

Solomon, F.N. & Ramnarine, I.W. 2007. Reproductive biology of white mullet, *Mugil curema* (Valenciennes) in the southern Caribbean. Fisheries Research, 88: 133-138. doi: 10.1016/j.fishres.2007.06.024

Somerton, D.A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Fisheries Research, 37: 1488-1494. doi: 10.1139/f80-192

Trippel, E.A. & Harvey, H.H. 1991. Comparison of methods used to estimate age and length of fishes at sexual maturity using populations of white sucker (*Catostomus commersoni*). Canadian Journal of Fisheries and Aquatic Sciences, 48: 1446-1459. doi: 10.1139/f91-172

Tsikliras, A.C., Stergio, K.I. & Froese, R. 2013. Editorial note on reproductive biology of fishes. Acta Ichthyologica et Piscatoria, 43: 1-5. doi: https://doi.org/10.3750/AIP2013.43.1.01

Valenciennes, A. 1836. Histoire naturelle des poissons. Tome onzième. Livre treizième. De la famille des Mugiloïdes. Livre quatorzième. De la famille des Gobioïdes. In: Cuvier, G. & Valenciennes, A. (Eds.). Histoire naturelle des poissons. Levrault, Paris.

Vasconcelos-Pérez, J., Sánchez-González, S. & Schultz-Ruiz, L. 1996. La pesquería de lisa. In: Sánchez-Palafox, A., Fuentes-Castellanos, D.F. & García-Real Peñaloza, S. (Eds.). Pesquerías relevantes de México. XXX Aniversario del INP. Instituto Nacional de Pesca, Ciudad de México, pp. 581-594.

Wallace, R.A. & Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in Teleosts. American Zoologist, 21: 325-343.

Zar, J.H. 2010. Biostatistical analysis. Prentice-Hall, New Jersey.