Latin American Journal of Aquatic Research, 51(4): 503-520, 2023
DOI: 10.3856/vol51-issue4-fulltext-3008

Research Article

Reproduction of *Lutjanus guttatus* (Perciformes: Lutjanidae) captured in the Mexican Central Pacific

Gabriela Lucano-Ramírez[1], Salvador Ruiz-Ramírez[1], Jorge A. Rojo-Vázquez[1]
Raúl E. Lara-Mendoza[2], Consuelo M. Aguilar-Betancourt[1] & Gaspar González-Sansón[1]
[1]Departamento de Estudios para el Desarrollo Sustentable de Zonas Costeras
Universidad de Guadalajara, Jalisco, México
[2]Departamento de Evaluación de Recursos Pesqueros en el Atlántico, Dirección de Investigación Pesquera en el Atlántico, Instituto Nacional de Pesca y Acuacultura, Ciudad de México, México
Corresponding author: Salvador Ruiz-Ramírez (salvador.ruiz@academicos.udg.mx)

ABSTRACT. Research on the reproduction of snappers helps to manage and conserve them. The spotted rose snapper *Lutjanus guttatus* is a gonochoric species caught year-round in Navidad Bay, Jalisco, Mexico. This work aims to analyze the reproductive aspects of the spotted snapper *L. guttatus* caught in Navidad Bay on the southern coast of Jalisco, Mexico. Analyzed fish came from commercial catches. Organisms were sampled monthly from January 1998 to December 2008, and total length, total weight, sex, gonad weight, and gonadal phase were obtained for each specimen. Histological analysis was performed to define the gonadal phase and measure the oocytes' diameter. The total length range in the catches was 14.0 to 61.0 cm; 2889 females and 2792 males were collected for a sex ratio 1.0:0.97. The oocyte development is asynchronous, with a diameter range from 33.9 to 407.9 µm. The testicle is of the lobular type, with a well-defined spermatic duct. A main reproductive season from June to September was identified, although fish with mature gonads were observed in all months. The best condition was observed before the reproductive period. Average lengths at sexual maturity were 30.09 and 30.05 cm for females and males, respectively; the average length of capture in females (32.2 cm) and males (31.7 cm) corresponds to 66.6 and 64.6% of organisms that had reproduced at least once before being captured. Given the importance and continuous capture of *L. guttatus* in the study area, we recommend further studies to improve the understanding of reproductive and fishing activities.

Keywords: *Lutjanus guttatus*; reproductive season; maturity size; sex ratio; gonadosomatic index; Mexican Pacific

INTRODUCTION

Snappers (Lutjanidae) are important in many tropical fisheries around the world. Many fisheries in these regions are mainly artisanal, making them more relevant as they benefit many people, either as a source of income or food (Polovina & Ralston 1987). According to FAO (2020), catches have had an annual average of 217,000 t worldwide for the past two decades. In Mexico, snapper fishing increased from 6701 t in 2009 to 19,065 t in 2018; in Jalisco (Mexico), fishing increased from 700 t in 2009 to 1115 t in 2018 (CONAPESCA 2018).

In the family Lutjanidae, the genus *Lutjanus* is the most diverse, including 73 of the 113 recognized species, with nine of these distributed in the eastern Pacific (Froese & Pauly 2019). Within this family, *Lutjanus guttatus* (Steindachner, 1869) inhabits the coastal zone from the Gulf of California, Mexico, to Peru. This species is an important fishing resource in

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Corresponding editor: Leonardo Abitia

several states along Mexico's Pacific coast (CONAPESCA 2018). Due to its catch volume, *L. guttatus* is one of the 10 most important species on the coast of Jalisco (Rojo-Vázquez & Ramírez-Rodríguez 1997, Rojo-Vázquez et al. 2001, 2008, Gómez-Vanega et al. 2021).

L. guttatus is a benthic carnivorous predator that feeds mainly on fish and small crustaceans (Saucedo-Lozano & Chiappa-Carrara 2000, Rojas-Herrera 2001, Rojas-Herrera & Chiappa-Carrara 2002, Flores-Ortega et al. 2010, Soto-Rojas et al. 2018); a species with a low growth rate (Rojas-Herrera 2001, Amezcua et al. 2006, Soto-Rojas et al. 2009, 2018). Reproductive activity can occur around the year, although with two main reproductive periods (Rojas 1997, Arellano-Martínez et al. 2001, Soto-Rojas et al. 2009, Sarabia-Méndez et al. 2010, Correa-Herrera & Jiménez-Segura 2013, Durán et al. 2020).

Despite the commercial importance of this species, there are few published studies on its biology, and its reproductive biology has never been studied in the area of our study. There is currently insufficient life history information on which to base a management strategy and stock assessment for this species on the coast of Jalisco and Colima, Mexico, and it is important to analyze basic reproductive aspects that help obtain good estimates of stock-based stocks. Inadequate estimations can lead to inappropriate stock assessment and regulatory measures, resulting in over or under-exploitation of the stocks (Laidig & Pearson 2003). This work aims to analyze the reproductive aspects of the spotted snapper *L. guttatus* caught in Navidad Bay on the southern coast of Jalisco, Mexico.

MATERIALS AND METHODS

Sampling

Specimens of spotted rose snapper *L. guttatus* were obtained from catches of commercial fisheries carried out on five days each month from January 1998 to December 2008. Small boat fishermen used gillnets of different mesh sizes in Navidad Bay, located on the south coast of Jalisco, Mexico (19°10′27″-19°13′18″N, and 104°41′54″-104°49′07″W; for details of the fishing area see Rojo-Vázquez et al. 2001) (Fig. 1). Total length (TL ± 0.1 cm), total weight (TW ± 0.1 g), sex and gonadal phase based on the morphochromatic scale of four phases of gonadal development following the criteria of Everson et al. (1989), which was identified by direct observation and were recorded for each organism. Gonads were removed, weighed (GW ± 0.01 g), and fixed in 10% neutral formalin for later histological analysis.

Histological sections were made (120 ovaries and 120 testicles) to describe the internal structure of the ovary and testis. A histological process was followed: dehydration with ethanol, including paraplast, obtaining 3 to 5 μm sections, and staining with Mallory's trichrome (Humason 1962). Sections were observed with a microscope (Primo Star, Zeiss) equipped with a digital camera (ERc 5s, Zeiss), and images and measurements of oocytes were obtained with the AxioVision program (V.4.8.2.0, Zeiss). The different oocyte phases were classified according to Yamamoto & Yamazaki (1961), Lucano-Ramírez et al. (2001a), and Brown-Peterson et al. (2011), and the testicle, according to the criteria of Lucano-Ramírez et al. (2001b) and Uribe et al. (2014, 2018).

Three types of data that complement each other were used to define the reproductive season. One is the gonadosomatic index ($GSI = [GW / (TW - GW)] \times 100$) (Everson et al. 1989), which is widely used as an indicator of the reproductive period under the assumption that the maximum average values indicate gonadal maturity (Sánchez-Cárdenas et al. 2007). The second data is the gonadal phases defined by the morphocromatic scale, considering the occurrence of organisms in developing, mature, and spawned phases as an indicator of the reproductive season. The third method analyzed the monthly variation of the average diameter of oocytes (DO), assuming that a greater average diameter corresponds to a greater degree of maturation of the ovary (West 1990, Lucano-Ramírez et al. 2014); thus, 30 oocytes per month of each development phases were randomly measured (maximum and minimum diameter of oocytes that presented a nucleus) (West 1990, Lucano-Ramírez et al. 2014). The relative condition factor ($CF = [TW / TL^{3.01}] \times 100$) was also obtained as an indirect indicator of the well-being of each organism (Le Cren 1951).

The length at which 50% of the individuals reached sexual maturity (L_{50}) was estimated for each sex, and the number of mature and immature organisms in each length class (4 cm intervals) was adjusted to the logistic model ($L_{50} = 1/ [1 + \exp^{bLT + a}]$) (Echeverria 1987). The fit was performed using a nonlinear approximation method (Levenberg-Maquart algorithm) (Statsoft 2006). The TL, TW, sex ratio, and L_{50} of each sex were analyzed for each year. The sex ratio was analyzed for the entirety of the sample, by month and by length class; the chi-square goodness-of-fit test (χ^2) with Yates' continuity correction (Zar 2010) was used to compare and determine if the sex ratio differs from the

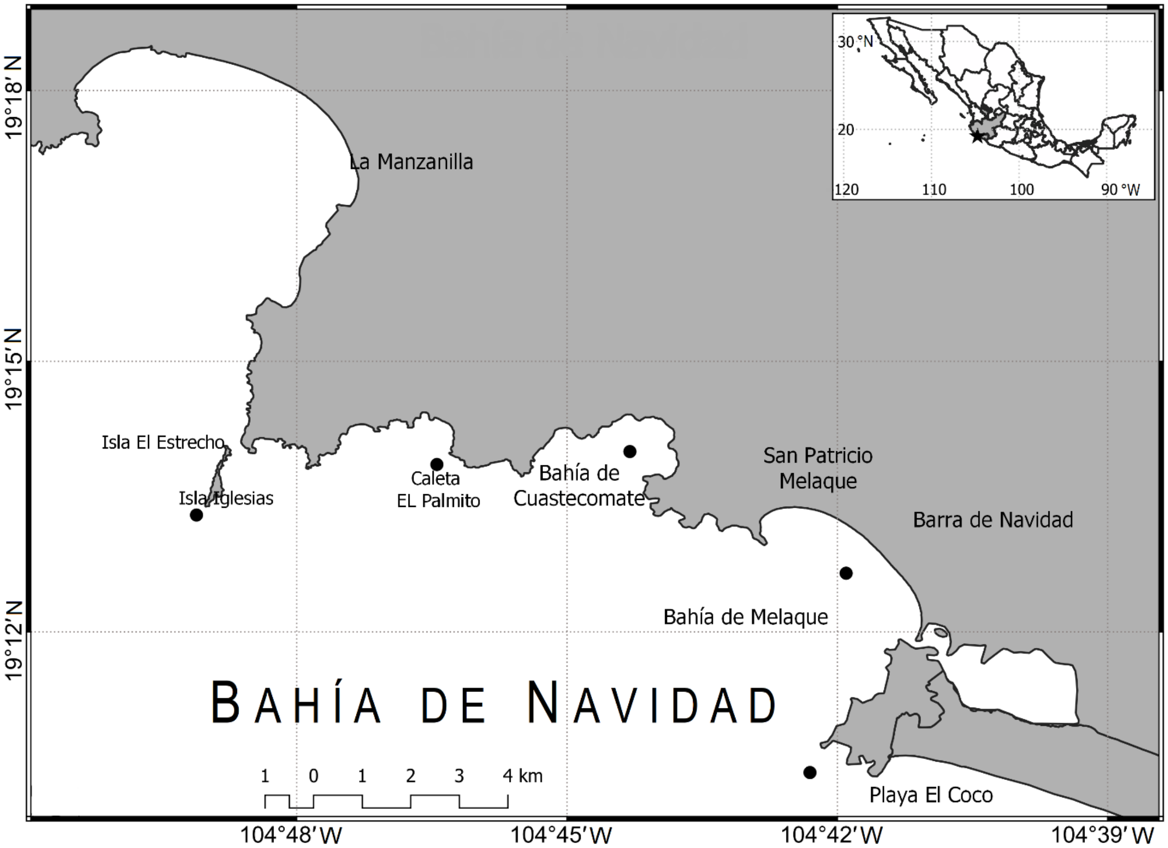

Figure 1. Study area, Bahía de Navidad, Jalisco, México.

expected sex ratio 1:1. A regression analysis was performed to evaluate the trend of change of the L_{50} in the 10 years; a single value of this parameter was obtained previously by combining the information of each sex.

Statistical analyses

Yearly changes in TL and TW were compared with a one-way analysis of variance (ANOVA). When the ANOVA showed a significant difference ($P < 0.05$), the Student-Newman-Keuls multiple-stage test (SNK) was applied (Zar 2010, Lucano-Ramírez et al. 2014). The monthly relationship between CF and GSI, and between GSI and mean oocyte diameter, was evaluated using Spearman's non-parametric rank correlation test (r_S) (Zar 2010, Lucano-Ramírez et al. 2014). Mean values are given along with their standard error (±SE). All the variables for analysis were grouped by month without considering the year because no important changes were observed between years, and to increase the sample size; with this, a standard year was integrated. The mean sea surface temperature values per month were obtained from a representative quadrant of the study area at coordinates 20-21°N and 103-105°W. These values were obtained from the internet page (http:/www.remss.com). Values of rainfall (mm) per month were obtained in the period 1998-2008 from the weather station "La Higuera," located in Tomatlán, Jalisco, belonging to the monitoring network of the National Meteorological Service of the National Commission of Water, SEMARNAT. A significance value of $\alpha = 0.05$ was used for all statistical analyses, and statistical tests were carried out in the Statistica v 7.1 program (Statsoft 2006).

RESULTS

In total, 5684 *L. guttatus* organisms were collected, presenting a mean TL of 31.9 (±0.09 SE) and an interval of 14.0 to 61.0 cm. Females had an average length of 32.2 ± 0.12 cm and males 31.7 + 0.12 cm; 83% of the organisms ranged from 24 to 36 cm. The frequency of females and males showed only small differences in most of the length classes (Fig. 2). In females and males, the annual analysis of the average TL showed a significant difference (Table 1); the minimum TL occurred in both sexes in 2003, and the maximum TL in both sexes occurred in 2005.

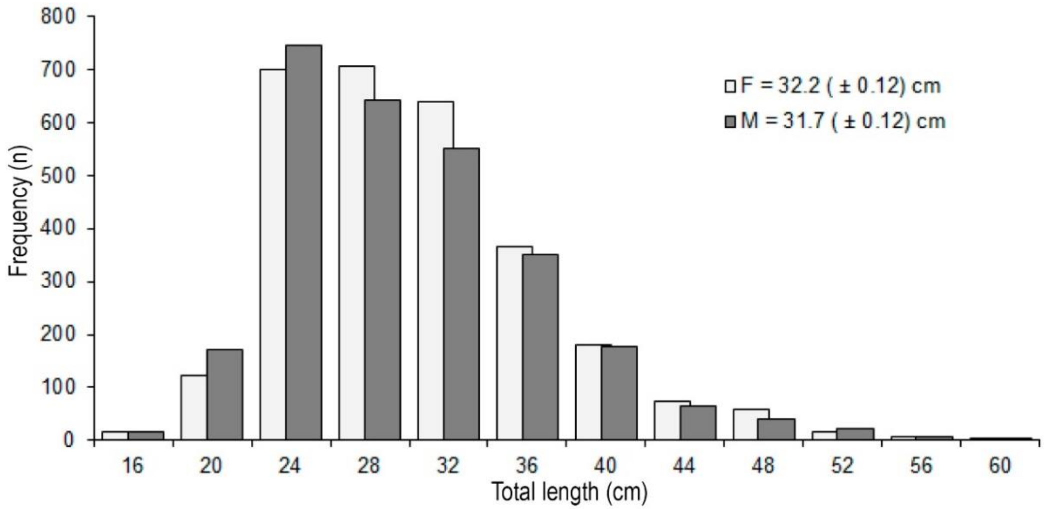

Figure 2. Total length frequency distribution of male and female *Lutjanus guttatus* captured in the central Pacific of Mexico. F: females, M: males.

Sex ratio

In total, 2889 females and 2792 males were analyzed. The sexual ratio was 1:0.97 (χ^2 = 1.66, P = 0.198), which does not differ significantly from the expected 1:1. The sex ratio showed differences just in lengths of 20 cm (χ^2 = 7.54, P = 0.006) and 32 cm (χ^2 = 6.51, P = 0.011); the number of males was greater in the first and females were more abundant in the second (Fig. 2). In 10 months of a total of 132, significant differences were found in the sex ratio; in 2000 there were differences in four months (June, July, September and November), in 1999 the difference occurred in two months (February and June). In 2002, 2003, 2007, and 2008 in a single month, there was a difference in the sex ratio (November, September, August, and September, respectively). By year, the proportion of sexes only showed significant differences in 2003 and 2006. By month, the sex ratio did not show a significant difference in any month (Table 2).

Ovary and testis characteristics

Table 3 describes some characteristics of the ovary and the testicle of *L. guttatus*. The ovarian wall, which covers the ovaries, is formed by muscular tissue (circular and transverse), and connective tissue, internally bordered by germinal epithelium, was 26.7 to 423.4 µm thick. The ovaries had a diameter of 1.9 to 15.6 mm. Six development phases of oocytes were distinguished simultaneously, suggesting an asynchronous development type with a size between 33.9 to 407.9 µm. The oocytes in primary growth had an average diameter of 65 ± 0.70 µm; these oocytes had a large nucleus compared to the cytoplasm, where the nucleoli, often located in the periphery of the nucleus, were observed. Oocytes had little cytoplasm and were abundant in immature ovaries (Figs. 3a-b). The cortical alveolus oocytes showed a 127 ± 1.81 µm diameter, with oil drops in the cytoplasm. In primary vitellogenesis, oocytes showed 198 ± 2.68 µm diameters with yolk globules in the cytoplasm. The oocytes in the secondary vitellogenesis stage measured 289 ± 2.97 µm, and the cytoplasm had many yolk globules (Figs. 3c-d). In the tertiary vitellogenesis stage, oocytes had 291 ± 4.67 µm diameters, and the cytoplasm showed fused yolk globules. The mature oocytes measured 270 ± 6.16 µm, and the cytoplasm showed fully fused yolk globules; the average diameter between the oocyte phases ($F_{5,\,1150}$ = 2,735 P < 0.001) showed a significant difference.

Due to the shape of the testicle, the diameter was not obtained. The internal organization of the testicle and the arrangement of the cells of the germ line follows a lobular-type pattern. Immature testicles showed a tunica albuginea, a distinguishable central efferent duct, and, in the periphery, cysts in different phases of development (Fig. 4a). Mature testes presented spermatozoa in the lobes' ducts, in the central efferent duct, and cysts in different phases of cellular development (Figs. 4b-c). Some spermatogenesis phases were distinguishable (Fig. 4d).

Reproductive season

Both sexes had immature and spawned phases present in all months with high percentages. In addition, both sexes showed fish in developing and mature phases for most months, though most occurred from April to

Table 1. Total length and weight (mean ± standard error), mean length at maturity (L_{50}) for each sex for *Lutjanus guttatus*. n: number of individuals. Values that do not have the same letter or have an asterisk indicate a significant difference. The values in parentheses indicate the range. *$P < 0.05$.

Variable	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	ANOVA
Females												
	n = 84	n = 196	n = 214	n = 144	n = 479	n = 185	n = 272	n = 216	n = 336	n = 423	n = 340	
Total length (cm)	30.8 ± 0.47^b	34.0 ± 0.39^{ef}	33.0 ± 0.42^{de}	34.1 ± 0.27^{ef}	28.7 ± 0.27^a	28.4 ± 0.47^a	32.3 ± 0.32^{cd}	35.4 ± 0.48^f	31.3 ± 0.25^{bc}	34.7 ± 0.32^f	32.8 ± 0.43^{de}	$F_{10,2878}$=42.06; $P < 0.001$
	(24.0-41.5)	(21.2-52.6)	(21.6-52.5)	(25.1-43.7)	(17.0-58.1)	(18.3-60.3)	(19.8-48.3)	(24.0-61.0)	(18.5-48.0)	18.2-57.0	(22.0-60.0)	
Total weight (g)	392.2 ± 18.0^{ab}	531.6 ± 16.0^{de}	502.4 ± 18.8^{cd}	502.3 ± 11.2^{cd}	330.1 ± 10.9^a	332.9 ± 21.3^a	439.8 ± 11.8^{bc}	608.2 ± 25.4^f	410.6 ± 9.8^b	578.6 ± 16.7^{ef}	509.5 ± 21.9^{cd}	$F_{10,2878}$=31.97; $P < 0.001$
	(183-900)	(133-1610)	(153-1657)	(210-981)	(77-2120)	(80-2600)	(99-1282)	(190-2580)	(84-1331)	(103-1940)	(136-2500)	
L_{50} (cm)	29.4	28.6	30.1	27.8	32.3	32.0	30.1	30.4	30.9	27.8	29.3	
Males												
	n =71	n =173	n =243	n =144	n =459	n =243	n =257	n =209	n =283	n =410	n =300	
Total length (cm)	30.1 ± 0.53^b	34.5 ± 0.42^d	33.9 ± 0.47^d	34.7 ± 0.31^d	28.3 ± 0.26^a	27.8 ± 0.38^a	31.0 ± 0.32^b	34.9 ± 0.47^d	30.5 ± 0.30^b	34.1 ± 0.33^d	32.2 ± 0.44^c	$F_{10,2781}$=49.33; $P < 0.001$
	(19.0-40.5)	(21.8-53.0)	(22.5-56.4)	(25.9-52.0)	(18.3-58.0)	(17.0-56.6)	(21.0-54.6)	(21.3-60.5)	(22.4-53.7)	(20.0-57.5)	(21.4-57.8)	
Total weight (g)	362.3 ± 17.1^{ab}	552.4 ± 19.1^{cd}	545.1 ± 22.3^{cd}	537.6 ± 15.1^{cd}	312.1 ± 10.2^a	304.9 ± 15.5^a	389.7 ± 12.6^b	578.8 ± 23.8^d	387.7 ± 12.1^b	542.2 ± 15.4^{cd}	479.9 ± 21.9^c	$F_{10,2781}$=37.77; $P < 0.001$
	(100-750)	(134-1730)	(134-2050)	(228-1646)	(85-2290)	(65-2041)	(126-2050)	(124-2500)	(143-1741)	(114-2028)	(123-2238)	
L_{50} (cm)	29.3	28.5	30.1	29.3	31.5	31.7	31.4	30.1	31.5	28.5	28.2	

September. The presence of individuals in the highest phases of maturation in all months suggests an almost constant, albeit low, reproductive activity for most of the year or throughout it (Fig. 5).

The monthly average values of the GSI presented significant variation in some months in females ($F_{11, 2877}$ = 2.86; P = 0.003) and males ($F_{11, 2779}$ = 2.99; P = 0.002). Females showed maximum values from July to September (group B) and low values in the rest of the months (group A). Males showed maximum values from May to September (group B) and lower values in the rest of the months (group A). The average values in the months, as mentioned earlier, were above the average values of the entire period for females (0.77) and males (0.54) (Fig. 6). The correlation between the GSI of females and males was significant (r_s = 0.85; P = 0.004; n = 12).

The monthly variation of CF in females ($F_{11, 2877}$ = 3.38; $P < 0.001$) and in males ($F_{1, 2780}$ = 4.93, $P < 0.001$) was significant. The highest average values in females and males were observed from April to July, a few months before the maximum GSI values. The CF of females correlated with that of males (r_s = 0.77; P = 0.003, n = 12). The CF and GSI correlated in males (r_s = 0.73; P = 0.006, n = 12); in females, although the CF and GSI appeared to have a similar temporal distribution, statistically, there was no correlation (r_s = 0.45; P = 0.14, n = 12) (Fig. 6).

The monthly average in oocyte diameter varied significantly ($F_{11, 1280}$ = 20.04; $P < 0.001$). The smallest diameters of oocytes occurred from January to April (group A) and the largest from June to September (groups BC and C), with subsequent decreases (October to December). The monthly trend of the diameter of oocytes significantly correlated (r_s = 0.83; $P < 0.001$, n = 12) with GSI (Fig. 7).

A significant difference was found between the average monthly sea surface temperature values ($F_{11, 120}$= 83.4, $P < 0.01$). In an annual cycle, the lowest sea surface water temperatures (less than 27°C; were recorded from January to April (groups A and B), and the highest temperatures (close to or greater than 29°C) from June to November (groups C-E) (Fig. 8). The rainfall was zero or low from January to April and in November and December; near or higher rains of 30 mm occurred from May to October, and the largest were presented from July to September (Fig. 8).

Length at maturity (L_{50})

The smallest adults with mature gonads had lengths of 29.80 cm (female) and 31.70 (male) cm TL. The estimated length at sexual maturity for females was

Table 2. Sex ratio by month for each year, by year, and per month (not considering the year) of *Lutjanus guttatus*. F:M = female:male, χ^2 values, *P* = probability, df: degree of freedom. Values in bold indicate a significant difference.

	1998			1999			2000			2001			2002			2003		
	F:M	χ^2	P	F:M	χ^2	P	F:M	χ^2	P	F:M	χ^2	P	F:M	χ^2	P	F:M	χ^2	P
January	1:0.0	0.00	1.00	1:1.0	0.17	0.68	1:0.3	2.13	0.14	1:1.1	0.15	0.70	1:0.8	0.49	0.48	1:0.0	0.00	1.00
February	1:0.5	1.11	0.29	1:0.0	**4.25**	0.04	1:1.2	0.31	0.58	1:0.0	0.00	1.00	1:1.3	2.25	0.13	1:0.0	0.00	1.00
March	1:2.3	1.70	0.19	1:1.2	0.26	0.61	1:0.9	0.27	0.60	1:0.9	0.05	0.82	1:1.7	1.06	0.30	1:0.0	0.00	1.00
April	1:0.4	1.70	0.19	1:0.5	0.67	0.41	1:0.0	0.00	1.00	1:0.0	0.00	1.00	1:1.0	0.50	0.48	1:0.0	2.00	0.16
May	1:1.0	0.25	0.62	1:0.8	0.90	0.34	1:1.1	0.47	0.49	1:0.8	0.75	0.39	1:0.8	0.60	0.44	1:0.0	2.50	0.11
June	1:1.2	0.45	0.50	**1:0.5**	**7.10**	**0.01**	**1:3.1**	**7.79**	**0.01**	1:2.7	2.36	0.12	1:0.8	2.71	0.09	1:1.4	3.27	0.07
July	1:0.3	3.08	0.08	1:1.8	0.91	0.34	**1:0.4**	**7.74**	**0.01**	1:0.0	0.00	1.00	1:0.9	0.10	0.75	1:0.0	0.00	1.00
August	1:0.9	0.20	0.65	1:1.2	0.47	0.49	1:1.0	0.06	0.81	1:0.0	0.00	1.00	1:1.2	1.35	0.25	1:1.9	2.17	0.14
September	1:0.7	0.40	0.52	1:1.0	0.07	0.79	**1:3.3**	**3.85**	**0.05**	1:0.0	0.00	1.00	1:0.8	0.18	0.67	**1:1.6**	**8.01**	**0.01**
October	1:0.0	2.50	0.11	1:0.9	0.25	0.62	1:1.4	0.65	0.42	1:0.0	2.50	1.00	1:1.3	1.26	0.26	1:1.0	0.03	0.86
November	1:0.4	1.70	0.19	1:0.0	0.09	0.76	**1:1.9**	**6.60**	**0.01**	1:0.0	0.00	0.11	**1:0.7**	**4.21**	**0.04**	1:0.9	0.41	0.52
December	1:2.0	0.83	0.36	1:0.9	0.00	1.00	1:0.8	0.30	0.58	1:1.0	0.00	1.00	1:0.8	1.02	0.31	1:0.0	2.00	0.16
Sex ratio	1:0.85			1:0.88			1:1.14			1:1.00			1:0.96			**1:1.31**		
χ^2	1.10			1.44			1.84			0.00			0.43			**7.86**		
P	0.29			0.23			1.75			1.00			0.51			**<0.01**		

	2004			2005			2006			2007			2008			Total		
	F:M	χ2	P	F:M	χ2	P	F:M	χ2	P	F:M	χ2	P	F:M	χ2	P	F:M	χ2	P
January	1:0.9	0.11	0.74	1:1.2	0.31	0.58	1:0.8	2.20	0.14	1:1.2	0.60	0.44	1:0.2	3.71	0.05	1:0.9	0.62	0.43
February	1:0.5	0.67	0.41	1:0.0	0.00	1.00	1:0.8	1.53	0.22	1:2.0	1.73	0.19	1:0.6	2.20	0.14	1:1.0	0.07	0.79
March	1:1.1	0.07	0.79	1:0.0	0.00	1.00	1:1.1	0.16	0.69	1:1.0	0.01	0.92	1:0.8	0.62	0.43	1:1.0	0.04	0.84
April	1:0.6	2.90	0.09	1:1.0	0.06	0.81	1:1.1	0.13	0.72	1:0.9	0.12	0.73	1:1.1	0.18	0.67	1:0.9	0.76	0.38
May	1:0.4	1.43	0.23	1:0.0	2.00	0.16	1:0.8	0.43	0.51	1:0.9	0.24	0.62	1:0.9	0.43	0.51	1:0.9	2.11	0.15
June	1:1.2	0.43	0.51	1:1.0	0.04	0.84	1:0.8	0.99	0.32	1:0.9	0.14	0.71	1:1.3	0.50	0.48	1:1.0	0.01	0.92
July	1:1.1	0.11	0.74	1:0.8	2.14	0.14	1:2.5	1.43	0.23	1:1.0	0.14	0.71	1:0.9	0.47	0.49	1:0.9	1.74	0.19
August	1:2.0	0.67	0.41	1:4.0	2.00	0.16	1:0.4	2.36	0.12	**1:0.2**	**12.48**	**0.01**	1:0.0	0.00	1.00	1:0.0	0.00	1.00
September	1:1.0	0.10	0.75	1:0.6	0.63	0.43	1:0.9	0.09	0.76	1:0.9	0.17	0.68	**1:8.0**	**5.56**	**0.02**	1:1.2	3.11	0.08
October	1:1.0	0.10	0.75	1:1.2	0.68	0.41	1:0.7	0.84	0.36	1:0.0	0.00	1.00	1:0.8	1.26	0.26	1:1.0	0.09	0.76
November	1:0.0	2.50	0.11	1:0.0	2.00	0.16	1:0.5	0.67	0.41	1:1.0	0.05	0.82	1:0.0	0.00	1.00	1:0.0	0.00	1.00
December	1:0.9	0.47	0.49	1:0.0	0.00	1.00	1:1.0	0.08	0.78	1:0.5	0.83	0.36	1:0.7	1.71	0.19	1:1.0	2.81	0.09
Sex ratio	1:0.94			1:0.97			**1:0.84**			1:0.97			1:0.88			1:0.97		
χ^2	0.43			0.12			**4.54**			0.17			2.50			12.98		
P	0.51			0.73			**0.03**			0.68			0.11			0.29		df = 11

30.09 cm and for males 30.05 cm TL; the average female length at capture (32.20 cm) and males (31.70 cm) corresponded to 66.6 and 64.6% of mature organisms, this indicates that more than 50% of the spotted snapper organisms collected in the commercial fishery had already reproduced at least once (Fig. 9).

The analysis of the annual variation of the length at maturity from 1998-2008 showed that the smallest L_{50} occurred in 2001 (26.6 cm TL) and the largest L_{50} occurred in 2002 (35.4 cm TL), whereas other years had values between 28.0 and 34.0 cm TL. For the 10 years, the regression analysis did not identify a clear trend ($F_{1,9}$ = 0.0002; P = 0.985); despite changes in some years, it seems that the L_{50} behavior is constant (Fig. 10).

DISCUSSION

Fishes' length is basic information in many studies (Franke & Acero 1992, Allen & Robertson 1998, Robertson & Allen 2015). This basic element provides additional information and serves as a reference for each species and is improved by the association of sex with length, as presented in other works on snappers such as *Lutjanus inermis* (Lucano-Ramírez et al. 2012, in Mexico) and *L. argentiventris* (Lucano-Ramírez et al. 2014, in Mexico). In this work, the length interval recorded for *L. guttatus* was close to that found in Rojas (1997) (12.16-60 cm TL, in Costa Rica), Correa-Herrera & Jiménez-Segura (2013) (18-58 cm TL, in Colombia) and Anderson (2005) (22-26 cm TL, in Panama). The proximity in the above lengths is interesting, considering the clear distance and geographical difference between study sites, and is probably caused by similarities in the fishing gear used by the commercial fisheries that caught the fish analyzed.

Table 3. Characteristics for each maturation phase of the ovary and testicle of *Lutjanus guttatus*.

Ovary in the immature phase	Testicle in an immature phase
The ovaries are small, thin, thread-like, translucent, pale, or dirty white with inconspicuous vascularisation. The ovaries occupy only a small part of the body cavity, and ova are not visible to the naked eye. Histologically, the ovary shows ovigerous lamellae, having nests of oogonia and primary growth oocytes (PG). No atresia or muscle bundles. Thin ovarian wall and little space between oocytes; there is scarce connective tissue between the follicles. The lumen is wide. Virgin	Testes are small, thin, flattened, and ribbon-like, more or less translucent (or opaque) with a smooth appearance. Only spermatogonia (Sg) present and cysts. No lumen in lobules. There are no spermatozoa (Sz) in any testicular área
Ovary in the developing phase	Testicle in the developing phase
Ovaries become slightly larger, thicker, opaque, and light yellowish. There is an increase in the weight of the ovary, and they cover a greater space in the body cavity. Blood vessels are becoming more distinct. Histologically, PG, cortical alveolar (CA), primary vitellogenesis (Vtg1), and secondary vitellogenesis (Vtg2) oocytes are present. No evidence of postovulatory follicle (POFs), tertiary vitellogenesis (Vtg3) oocytes, or atresia. Increases the thickness of the ovary wall	Testes are increasing in size and triangular in cross-section, whitish color. The sperm does not flow with pressure. Larger than immature gonads. Spermatocysts are evident along lobules. Sg, spermatocyte (Sc), spermatid (St), and Sz can be present in spermatocytes. Sz is absent in the lumen of lobules or sperm ducts or just a little.
Ovary in a mature phase	Testicle in a mature phase
The ovaries are further enlarged, occupying a large part of the body cavity. They are turgid and yellow, and many spherical ova, both translucent and opaque, are present and visible to the naked eye through the thin ovarian wall. The blood supply increases considerably, and the ovary attains its maximum weight. In this phase, ova are sometimes extruded by applying gentle pressure on the abdomen. Histologically, immature oocytes are reduced in number, while a large number of Vtg2 and Vtg3 in stage VII, and germinal vesicle breakdown (GVBD), germinal vesicle migration (GVM), and oocyte maturation (OM).	Large and firm testes well developed, with conspicuous superficial blood vessels; whitish-pinkish color: abundant spermatids and some spermatozoa within seminiferous tubules. The sperm duct is relatively full of sperm. All stages of spermatogenesis (Sg, Sc, St, and Sz) can be present. Spermatocysts throughout testis, active spermatogenesis. Accumulation of sperm in the spermatic ducts, sperm flows with low pressure
Ovary in spawned phase	Testicle in spawned phase
The ovaries are flaccid, shrunk, and sac-like, reduced in volume, and have a dull color. The vascular supply is present but is reduced. The weight of the ovary decreases. Some unspawned large ova and a large number of small ova are present. Histologically, the ovary shows some CA or Vtg1, Vtg2, atresia (any stage), and POFs, but not GVBD, GVM, and OM. Muscle bundles and thick ovary wall	Testes are flaccid and bloodshot, pinkish. Sperm may still flow (only a small quantity). Residual Sz is present in the lumen of lobules and sperm ducts. Widely scattered spermatocytes near the periphery containing Sc, St, and Sz. Little to no active spermatogenesis

Sex ratio

In the present work, no significant difference was found in the sexual proportion for the total *L. guttatus* organisms captured. This result was similar to those obtained for this species in Guerrero, Mexico, (0.96F:1M) (Arellano-Martínez et al. 2001) and (0.92F:1M) (Rojas-Herrera 2001); in Nicoya, Costa Rica, (1F:1M) (Soto-Rojas et al. 2009) and in the Gulf of California, Mexico, (1F:1M) (González-Ochoa et al. 2009). This same trend has been recorded in other snappers, such as *L. inermis* (1F:0.88M) (Lucano-Ramírez et al. 2012) and *L. argentiventris* (1F:0.99M) (Lucano-Ramírez et al. 2014), both in Jalisco, Mexico. Conversely, two studies on this species recorded a greater number of males than females: the first (1F:1.5M) in Nicoya, Costa Rica (Rojas 1997) and the second (1F:1.5M) in Utría, Colombia (Correa-Herrera & Jiménez-Segura 2013). It is not always possible to realistically represent the sex ratio of a fish population, as this can be associated with differences in habitat

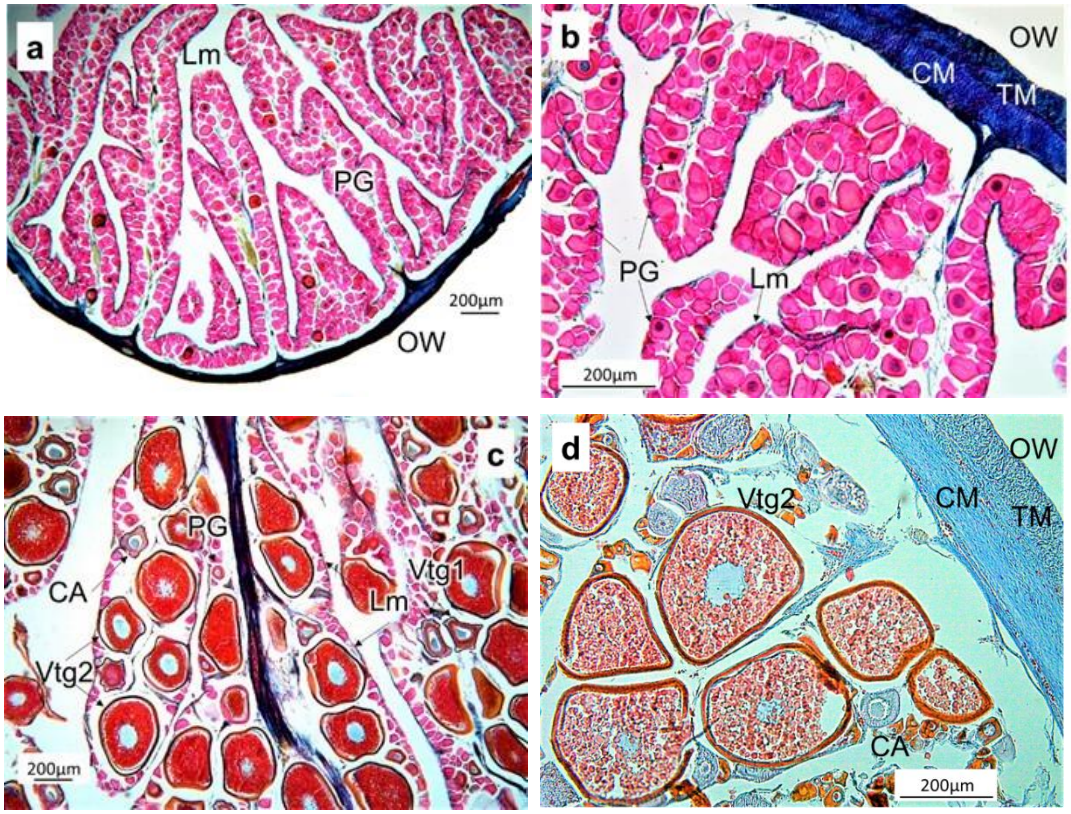

Figure 3. Cross section of the ovary of *Lutjanus guttatus*. a) Immature ovary with ovarian wall (OW) and oocytes in primary growth (PG) grouped by the lamellae (Lm) (4x), b) ovarian wall formed by connective tissue, circular muscular tissue (CM), transverse muscular tissue (TM) and groups of oocytes in primary growth (10x), c) mature ovary with oocytes in asynchronous development: primary growth (PG), cortical alveoli (CA), primary vitellogenesis (Vtg1) and secondary vitellogenesis (Vtg2) (4x), d) mature ovary with ovarian wall where the two types of muscle tissue and oocytes in different stages are differentiated (10x). Mallory's trichrome stain.

preference exhibited by each sex and can vary during an annual cycle (García-Cagide et al. 1999).

For various species of Pacific snapper, for which information is available (aforementioned), it can generally be concluded that there is no clear dominance of one sex over the other. Thus, fishing is not aimed at capturing a single sex; therefore, this activity does not appear to affect local snapper populations in this respect.

It has been mentioned that the sex ratio in snappers tends to balance out during spawning (Grimes 1987, García-Cagide et al. 1999, Soto-Rojas et al. 2009), and it seems that this could occur in *L. guttatus* since no difference was found in the sexual ratio during the reproductive season.

Macroscopic and microscopic characteristics of the gonads

All species of the genus *Lutjanus* are gonochoric. Each sex occurs in separate organisms (Claro & Lindeman 2008). This characteristic has been confirmed for *L. peru* (Lucano-Ramírez et al. 2001b), *L. inermis* (Lucano-Ramírez et al. 2012), *L. argentiventris* (Lucano-Ramírez et al. 2014) and *L. guttatus* (Arellano-Martínez et al. 2001) and in the present study.

Including the present work, the functional morphology of snapper gonads follows the common pattern of teleosts (Wallace & Selman 1981, De Vlaming 1983, Nagahama 1983). Snappers do not show sexual dimorphism, and sexes can only be identified by gonadal inspection because the shape, size, texture, and color of the gonads are different in males and females (Claro & Lindeman 2008).

In snappers, research on the microscopic description of the ovary is scarce. The ovarian wall, which surrounds the ovary, is made up of muscle and frequently enters the ovary to form the lamellae, inside which the oocytes develop; it also serves to delimit groups of oocytes. Lucano-Ramírez et al. (2001a) descri-

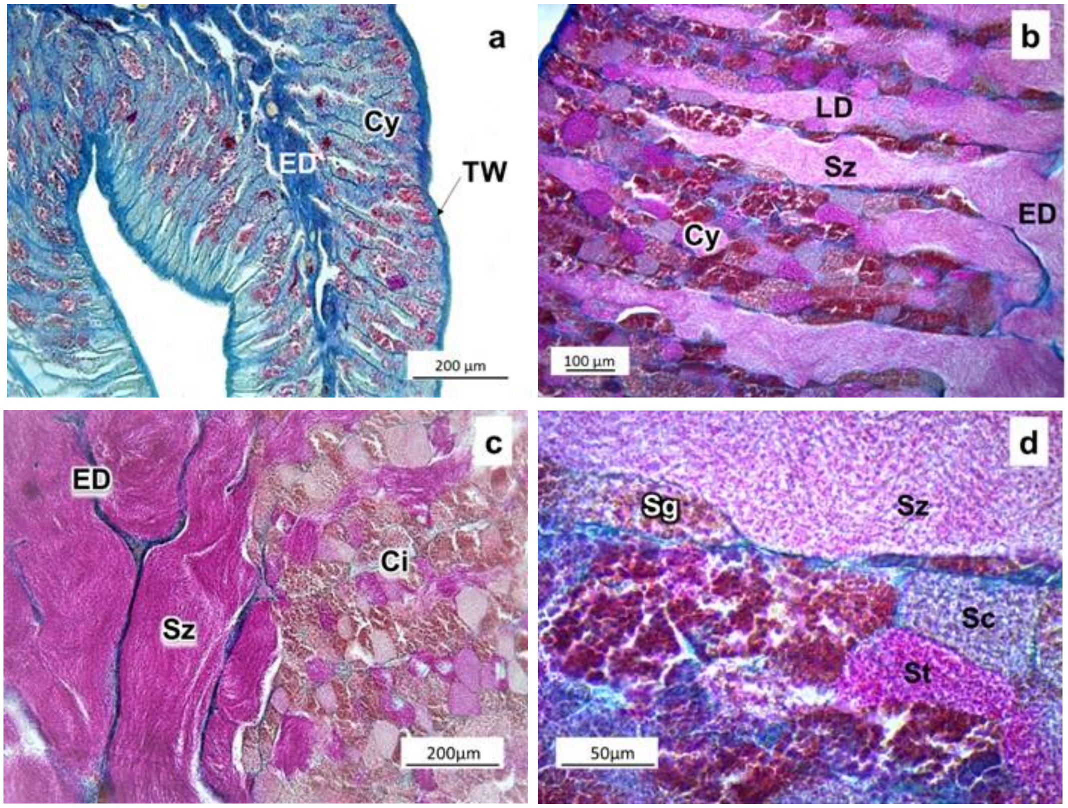

Figure 4. Cross section of the testis of *Lutjanus guttatus*. a) Immature testis with cysts (Cy) in different stages of cell development, central efferent duct (ED), and testicular wall (TW) (10x), b) mature testicle with spermatozoa (Sz) in the ducts of the lobes (LD) and the central efferent duct (ED), cysts in different stages of cell development (10x), c) central efferent duct and lobes with spermatozoa, cysts in different stages of cell development (10x), d) germinal compartment with several cysts in different stages of cell development: spermatogonia (Sg), spermatocytes (Sc), spermatids (St) and spermatozoa in the central efferent duct (40x). Mallory's trichrome stain.

bed the ovarian wall of *L. peru* as having two types of muscle, one circular and the other longitudinal; this characteristic was also observed in the present study. Cerisola (1984) identified the same elements in the ovarian wall for *Sicyases sanguineus*. González et al. (1979) mention that the ovary in *Lutjanus griseus*, in Cuba, had a thin wall with thickness between 90.0 and 310.0 µm; these values are close to those observed in *L. peru* (Lucano-Ramírez et al. 2001a), with thickness between 22.5 to 392.0 µm, and in *L. guttatus* in this work, with thickness between 26.7 to 423.4 µm.

In several species of lutjanids, the histology of the mature ovary shows the simultaneous presence of several phases of oocyte development. This characteristic is typical in species with an asynchronous development type (Arellano-Martínez et al. 2001). This trait seems to be a common pattern in snappers that are distributed in the tropical central Pacific, such as *L. peru* (Lucano-Ramírez et al. 2001a, Rojas-Herrera 2001, Santamaría-Miranda et al. 2003), *L. guttatus* (Rojas 1997, Arellano-Martínez et al. 2001, Rojas-Herrera 2001, Piñón-Gimate 2003, and this study), *L. colorado* (Piñón-Gimate 2003), *L. argentiventris* (Piñón et al. 2009, Guerrero-Tortolero et al. 2010, Lucano-Ramírez et al. 2014) and *L. inermis* (Lucano-Ramírez et al. 2012). Rojas (1997) and Arellano-Martínez et al. (2001) mention that *L. guttatus* performs partial spawning because they observed ovaries with oocytes in advanced development stages and postovulatory follicles. Nagahama et al. (1995) and Maack & George (1999) consider that species that present oocytes with asynchronous development generally spawn several times in a reproductive season, which tends to be prolonged, which could occur in *L. guttatus* since it has oocytes with asynchronous development and has a prolonged reproductive season.

The temporal variation of the average diameter of the oocytes is a variable that can be used to reinforce

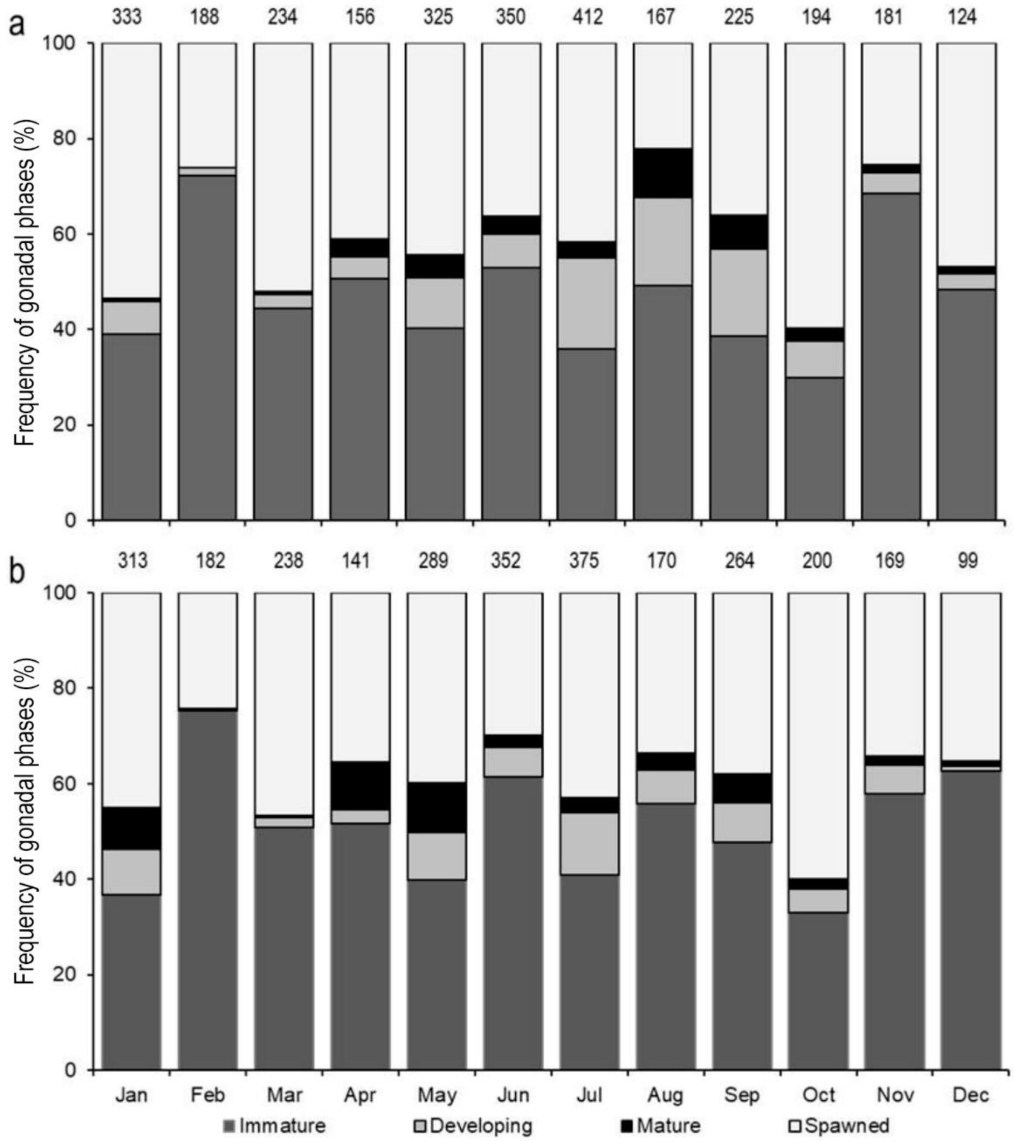

Figure 5. Frequency of gonadal phases in a) females and b) males of *Lutjanus guttatus* captured in the central Pacific of Mexico.

the reproductive period found in fishes, and, in this case, *L. guttatus* showed temporal coincidences between the maximum values of the diameter of oocytes, high values of GSI and presence of the mature stage. The analysis of these three aspects has also been used in *L. argentiventris* (Lucano-Ramírez et al. 2014), *Carangoides vinctus* (Lucano-Ramírez et al. 2016), *Epinephelus labriformis* (Ruiz-Ramírez et al. 2019), *Achirus mazatlanus* (Lucano-Ramírez et al. 2019) and *Mulloidichthys dentatus* (Lucano-Ramírez et al. 2019); the temporal association of these three variables can help to define the reproductive period in fishes with greater certainty.

Histology of the testis was used to identify the development stage of cells. The cellular organization is like in most teleosts, and the spermatogonia are located throughout the lobes. In addition, spermatogenic development within the cysts is synchronous, and lobes are found at different degrees of development (Grier 1981, Van Tienhoven 1983, Arellano-Martínez et al. 2001, Uribe et al. 2018). Several species of teleosts exhibit a lobe-type testicle; among these are *L. peru* (Lucano-Ramírez et al. 2001b), *L. guttatus* (Arellano-Martínez et al. 2001), *L. inermis* (Lucano-Ramírez et al. 2012) and *L. argentiventris* (Lucano-Ramírez et al. 2014).

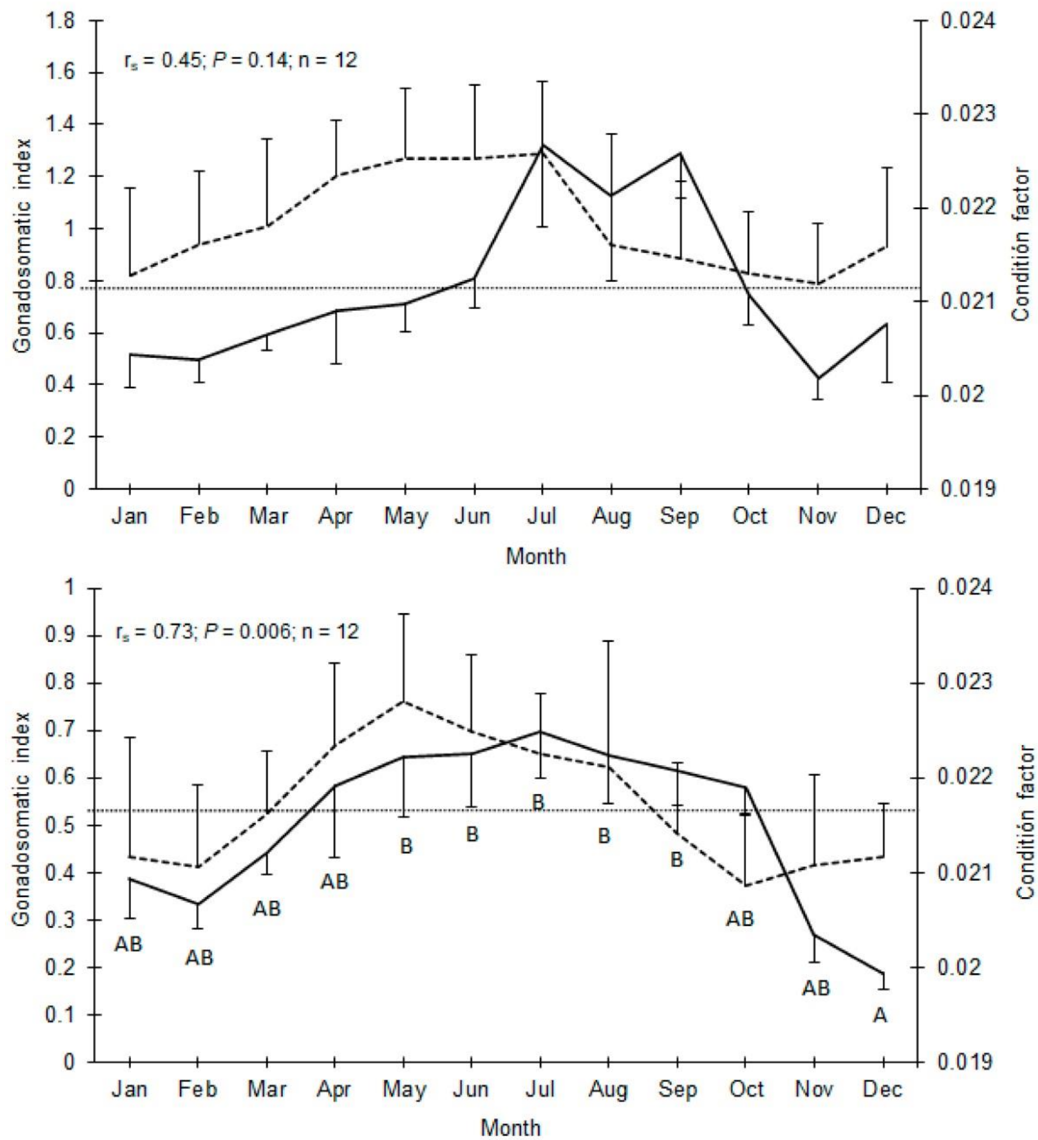

Figure 6. Monthly variation of the gonadosomatic index (continuous line) and the condition factor (dashed line) (mean ± standard error) of a) females and b) of *Lutjanus guttatus* captured in the central Pacific of Mexico. The transverse line represents the average value of the gonadosomatic index.

Reproductive season

The length of the breeding season, the type of spawning, and the latitude where it takes place are all associated. For species that inhabit high latitudes, the summer period is short, and spawning is generally short, total, and well-established (Cushing 1975, Blaxter & Hunter 1982). The reproductive period is longer for fish in tropical and subtropical latitudes. Spawning is partial or may occur throughout most of the year (Cushing 1975), which seems to be the case in several snapper species such as *L. peru* (Lucano-Ramírez et al. 2001b, Rojas-Herrera 2001, Santamaría-Miranda et al. 2003), *L. argentiventris* (Piñón et al. 2009, Lucano-Ramírez et al. 2014), *L. inermis* (Lucano-Ramírez et al. 2012) and *L. guttatus* (Rojas 1997, Arellano-Martínez et al. 2001, Rojas-Herrera 2001, and this study).

The asynchronous growth of oocytes supports a prolonged reproductive period in lutjanid species, which is the key to fractional spawning (Claro & Lindeman 2008). *L. guttatus* also showed this characteristic in this study. One strategy that snappers follow is to combine long reproductive periods, high fecundity, and the production of small-diameter eggs (Rojas-Herrera 2001). In this work, *L. guttatus* shared the strategies mentioned above.

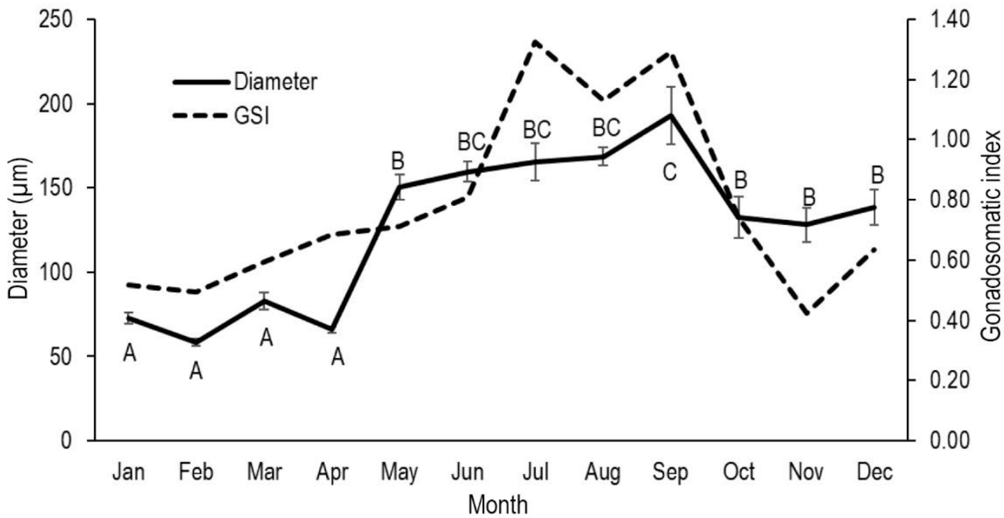

Figure 7. Gonadosomatic index and oocyte diameter per month (mean ± standard error) of *Lutjanus guttatus*. Means that do not have the same letter are significantly different ($P < 0.05$).

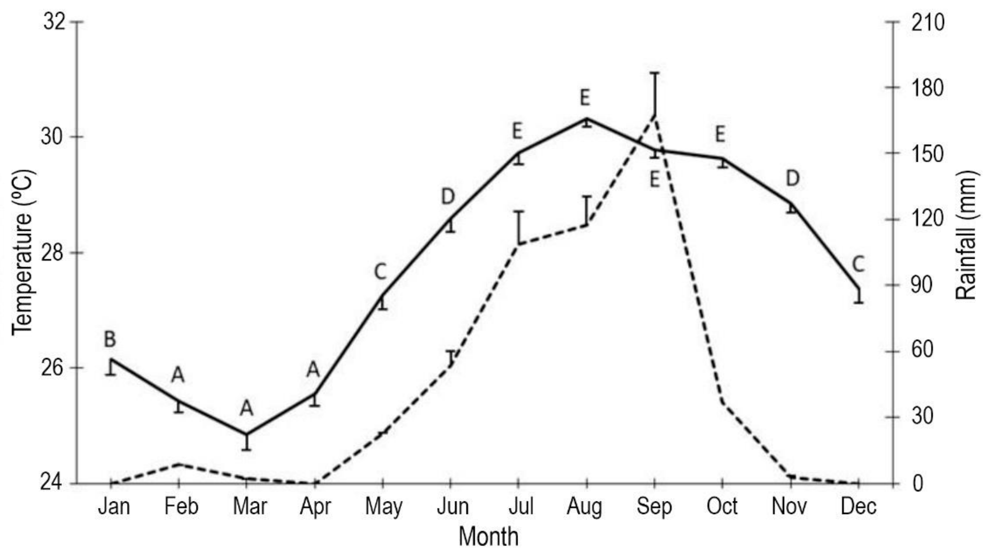

Figure 8. Monthly variation of temperature (continuous line) and rainfall (dashed line) (mean ± standard error) on the coast of Jalisco, Mexico. Means that do not have the same letter are significantly different ($P < 0.05$).

Macroscopic characteristics that describe the gonads and GIS have been used to establish the reproductive period of many fish species, including snappers (West 1990, García-Cagide et al. 2001). The GSI is used to establish reproductive periods in various snapper species (Arellano-Martínez et al. 2001, Rojas-Herrera 2001, Santamaría-Miranda et al. 2003, Piñón et al. 2009, Soto-Rojas et al. 2009, Lucano-Ramírez et al. 2012, 2014, Correa-Herrera & Jiménez-Segura 2013). In this study, as well as in Colima (Cruz-Romero et al. 1996) and Guerrero (Arellano-Martínez et al. 2001), Mexico, and Costa Rica (Soto-Rojas et al. 2009), *L. guttatus* showed mature gonads for all or most of the year. Nonetheless, the authors point out that the species showed two main reproductive periods: March-April and August-November, which showed high percentages of mature and spawning gonads and coincided with high GSI values. In this work, GSI increased in July-September, similarly to the sea surface temperature, and coincided with the rainy season when runoff increases the amount of sediment and, thus, the production that results from rainwater discharges (Martínez-Flores et al. 2011).

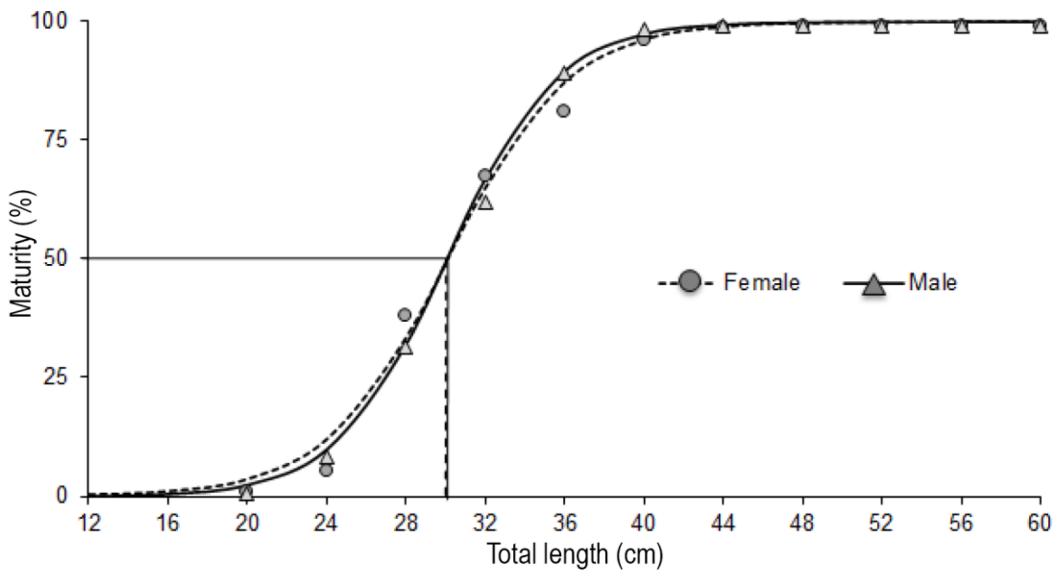

Figure 9. Percentage of matured females and males of *Lutjanus guttatus* captured in the central Pacific of Mexico. Values adjusted to the logistic equation.

For some species, the GSI does not show a clear trend in an annual cycle, and the complementary microscopic analysis of the gonads makes it possible to identify reproductive periods more clearly (West 1990, Arellano-Martínez et al. 2001, Rojas-Herrera 2001, Teixeira et al. 2010). This study analyzed the microscopic characteristics of the gonads, the variation of gonadal maturation phases, the GSI, and the average diameter of the oocyte to establish the reproductive period. Piñón et al. (2009) mentioned that studies that analyze the flexibility of the reproductive period in lutjanids are required to verify if spawning occurs in months in which the ovaries have a high percentage of vitellogenic oocytes.

Condition factor (CF)

CF is considered a good indicator of physiological conditions in fish and is often used to compare physiological and reproductive conditions. In *L. guttatus*, GSI and CF showed the same trend (Arellano-Martínez et al. 2001). In the present work, females and males of *L. guttatus* also showed this trend, suggesting that the organisms were apt to carry out the reproductive process. Furthermore, in the study region, coastal upwelling occurs as a result of the prevailing winds from the northwest (Ambriz-Arreola et al. 2012, 2018, Kozak et al. 2017), which can have a benefit in the body condition of *L. guttatus*.

The maturation of the oocytes requires considerable energy resources to supply the substances needed to nourish and develop the embryo in the future. Therefore, vitellogenesis usually occurs after an accumulation of reserves in the organism, both as lipids and protein (Rojas-Herrera 2001). Female *L. guttatus* showed high CF values before the reproductive period; this helped to obtain nutrients to develop and mature gonads.

Length at maturity

Sexual maturity in snappers occurs when they reach a length between 40 and 50% of the maximum length, with insular populations and species of this family maturing at a greater length (51% of the maximum length) than oceanic ones (43%) (Grimes 1987). Considering the maximum length reported for *L. guttatus* (80 cm; Allen & Robertson 1998) and the percentage mentioned by Grimes (1987) for oceanic snappers, the estimated L_{50} in *L. guttatus* is several centimetres less than that indicated by Grimes (1987). *L. guttatus* is a species that inhabits shallow depths and reaches sexual maturity at between three and four years of age (Piñon-Gimate 2003), probably due to a balance between life cycle factors (differentiation processes and reproduction), abiotic factors (temperature, photo-period, nutrients, primary productivity, and feeding) and physiological factors (energy distribution between somatic and reproductive growth) (Grimes 1987, Rojas 1997). Several studies have estimated L_{50} for *L. guttatus*, some of these works (five out of nine) coincide or are close (in less than 4 cm TL) to the L_{50}

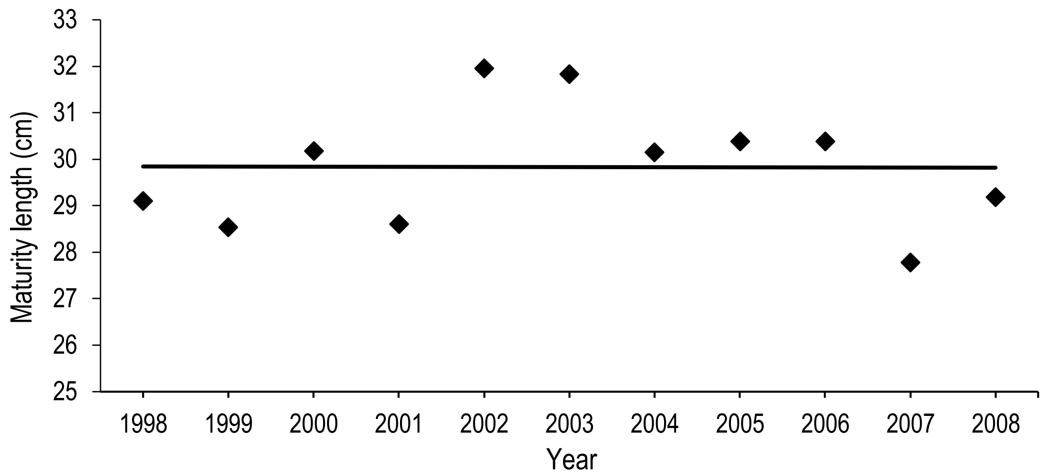

Figure 10. Annual variation of the length at maturity (L_{50}) of *Lutjanus guttatus* captured in the central Pacific of Mexico. The line represents the temporal trend of L_{50}.

Table 4. Length at maturity for *Lutjanus guttatus* at different sites in Mexico and other countries. TL: total length, FL: fork length. *Minimum length of maturation.

Site	Maturity length (cm)	Reference
Sinaloa, Mexico	29.8 (female) TL	Piñon-Gimate (2003)
Jalisco, Mexico	29-34 TL	Rojo-Vázquez et al. (1999)
Colima, Mexico	17-18 TL	Cruz-Romero et al. (1996)
Michoacán, Mexico	30.6 TL	Sarabia-Méndez et al. (2010)
Guerrero, Mexico	23.5 FL	Rojas-Herrera (2001)
Costa Rica	31.7-34.3 TL	Rojas (1997)
Panama	39.66 (female) and 36.13 (male) TL	Durán et al. (2020)
Jalisco, Mexico	30.09 (female) and 30.05 (male) TL	This study

estimated in the present work; two studies used a different reference length (fork length) that may partially explain the differences with the majority of studies (Table 4). Although some studies used the same method to estimate the L_{50}, certain differences are observed; this may be caused by the unsuitable use of maturation phases and the sole use of observations of macroscopic characteristics of the gonads. The present work used the macroscopic and microscopic characteristics of gonads.

Few studies have analyzed the variation of the L_{50} in the medium and long term. The present study identified no notable change in the trend of the L_{50} in *L. guttatus*. It could result from only analyzing organisms from commercial fisheries, the species continuing to reproduce at a similar length interval year after year, for a reason unknown until now, or the fishing activity needing to be more intense to cause a decrease in the L_{50}. Conversely, some studies have indicated that fishing pressure has partially influenced the decrease in L_{50} in some stocks and species (Trippel 1995, Hunter et al. 2015). Given the importance and continuous capture of *L. guttatus* in the study area, we recommend further studies to improve the understanding of reproductive and fishing activities.

In summary, *L. guttatus* is a dioecious species that presents an ovary with asynchronous development; this supports that the species reproduces for a large part of the year with a main period from June to September. The best body condition occurs before this period. The region's rainy and hurricane seasons can influence this species' reproductive period. Although the trend in the length of maturation did not present a clear decline and although a large part of the organisms captured would have already had at least one reproductive event, it is suggested to include preventive measures as this is a species with great commercial interest and a sustained high level of capture.

ACKNOWLEDGMENTS

To the University of Guadalajara for the financial resources to develop this research. To the fishing cooperatives "Rivera de Melaque" and "Punta Farallón" for facilitating sampling facilities to fishermen who collaborated monthly to capture the organisms. To all the students who participated in the fieldwork.

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Received: November 10, 2022; Accepted: April 28, 2023

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