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Reproduction of grey snapper (Teleostei: Lutjanidae) in the southern Gulf of Mexico

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Summary: Snappers exhibit reproductive trait plasticity in response to habitat distribution. *Lutjanus griseus* is among the most economically important snappers in the western Central Atlantic but has received limited study in the region. Data on the reproductive biology of the *L. griseus* population were collected on the continental shelf of the Yucatan Peninsula, Mexico. Over a nineteen-month period, 1236 specimens were captured monthly in three Yucatan artisanal fishing fleet operational areas. Data were grouped by month to generate an annual analysis. Individual sex and maturation status were identified by gonad histology. Median size did not differ between females (33.2 cm fork length [FL]) and males (33.3 cm FL), and the sex ratio was balanced (F:M=0.98:1.00). Size at maturity was 24.2 cm FL for females (38% of maximum size reported for the species) and 22.8 cm FL for males (36% of maximum size), and the spawning season ran from May to September. The results confirm that this population exhibits the typical reproductive pattern of snappers distributed on continental shelves or in shallow water areas and provide critical data for stock assessment and implementation of management measures for *L. griseus* stock in the southern Gulf of Mexico.

Keywords: sex ratio; sexual maturity; spawning season; Lutjanidae; Mexico.

Reproducción del pargo gris (Teleostei: Lutjanidae) en el sur del Golfo de México

Resumen: Los pargos exhiben plasticidad en sus rasgos reproductivos según su hábitat de distribución. *Lutjanus griseus* es uno de los pargos de mayor interés económico en el Atlántico Central Occidental, pero ha sido poco estudiado en esta región. Este trabajo analiza la biología reproductiva de la población de *L. griseus* de la plataforma continental de la Península de Yucatán, México. En un periodo de un año y medio natural se capturaron 1236 especímenes en tres áreas operativas de la flota pesquera artesanal de Yucatán. Los datos fueron agrupados por meses para generar un análisis anual. El sexo y el estado de maduración de cada individuo fueron determinados mediante el análisis histológico de sus gónadas. No se observó una diferencia significativa entre las medianas de las tallas de las hembras (33.2 cm LF) y de los machos (33.3 cm LF), y la proporción sexual fue equilibrada (H:M=0.98:1.00). Los datos obtenidos sobre las tallas de madurez fueron de 24.2 cm LF para las hembras (38% de la talla máxima de la especie) y de 22.8 cm LF (36% de la talla máxima) para los machos y la temporada de desove ocurrió entre mayo y septiembre. Estas características confirmaron que la población presenta el patrón de reproducción típico de los pargos distribuidos en plataformas continentales o en zonas de agua somera. Estos resultados proporcionan datos críticos para la evaluación y la aplicación de medidas de gestión de la población de *L. griseus* del sur del Golfo de México.

Palabras clave: proporción sexual; madurez sexual; temporada de desove; Lutjanidae; México.

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INTRODUCTION

Snappers (Lutjanidae) are mainly restricted to tropical and subtropical regions. They are commercially important fish species throughout their geographical range, especially for local artisanal fisheries (Allen 1985). Snapper populations in the Gulf of Mexico are distributed over extensive continental platforms, while those of the Caribbean Sea are essentially insular (Allen 1985, Bannerot et al. 1987). The grey snapper *Lutjanus griseus* (Linnaeus, 1758) is widely and continuously distributed from Massachusetts in the United States to the Caribbean coast of Venezuela (Lindeman et al. 2016). It is one of the most abundant reef fish in many areas of the Caribbean Sea. In Florida, it represents a major portion of recreational snapper catches; indeed, the *L. griseus* recreational fishery in this region exceeds its commercial fishery in terms of catch (Allen 1985, Lindeman et al. 2016). Although the International Union for Conservation of Nature (IUCN) Red List classifies *L. griseus* as of least concern, Lindeman et al. (2016) argue that its populations in Cuba, Puerto Rico and along the US Atlantic coast show signs of decline. In the northern Gulf of Mexico, the US stock is not considered to be overfished but has exhibited signs of overfishing since 1976 (SEDAR 2018). In the southern Gulf of Mexico, *L. griseus* is one of the main snapper species exploited by artisanal fishers in the state of Yucatan, Mexico (Monroy-García et al. 2019). Snapper fisheries have become increasingly important in Yucatan in response to sharp declines in populations of red grouper *Epinephelus morio* (Valenciennes, 1828), the region's main fishery. In addition, large decreases have been observed in the population of Mexican red snapper *Lutjanus campechanus* (Poey, 1860) since early 1990 (SAGARPA 2018). Both trends have helped make *L. griseus* one of the most exploited snappers in the waters of the Yucatan Peninsula (Monroy-García et al. 2019).

In response to their distribution habitat, snappers generally show a certain plasticity in some of their reproductive traits. Following Grimes' (1987) concept, reproductive seasonality and size at maturity in snappers are more dependent on habitat types than on latitude. Species or populations that inhabit continental shelves or shallow waters (<91 m) have a restricted spawning season centred in summer and a sexual maturity which occurs at 41% (continental shelves) or 43% (shallow waters) of species maximum size. Conversely, species or populations from insular regions or deep reef zones (>91 m) reproduce year-round with spawning pulses in spring and autumn, and experience sexual maturity at 51% (insular regions) or 49% (deep reef zones) of species maximum size (Grimes 1987). For example, the population of silk snapper *Lutjanus vivanus* (Cuvier, 1828) from North Carolina and South Carolina has a restricted spawning season (June to August) and matures at 36% (female) or 41% (male) of its maximum size, whereas in Jamaica the same species spawns year-round and matures at 85% (female) or 73% (male) of its maximum size. In the Antilles and the Bahamas, deepwater (120-180 m depth; Allen 1985) black snapper *Apsilus dentatus* (Guichenot, 1853) mature at 74% (female) or 79% (male) of its maximum size (Grimes 1987). However, Grimes (1987) also mentions that in various snapper populations around the world, sexual maturity and/or reproductive season are not strictly dictated by habitat type. For example, populations of red snapper *L. campechanus* and yellowtail snapper *Ocyurus chrysurus* (Bloch, 1791) from the continental shelf of the Yucatan Peninsula are reported to have an extended seasonal reproductive pattern: February to November for *L. campechanus* (Brulé et al. 2010) and January to September for *O. chrysurus* (Trejo-Martínez et al. 2011). This is more typical of insular snapper species and populations.

The reproductive biology of *L. griseus* has been investigated in populations in Florida (Starck 1971, Domeier et al. 1996, Allman and Grimes 2002), Cuba (González et al. 1979, Báez et al. 1982, Claro 1983), Guatemala (Andrade and Santos 2019) and Venezuela (Guerra-Campos and Bashirullah 1975), but not in the southern Gulf of Mexico. Therefore, the present study analysed the main reproductive characteristics (sex-size distribution, sex ratio, size at maturity and spawning seasonality) of *L. griseus* from the continental shelf of the Yucatan Peninsula (i.e. Campeche Bank). The objective was to assess whether this population exhibits the pattern of sexual maturity and reproductive seasonality typical of continental snapper species and populations.

MATERIALS AND METHODS

Study area

In the southern Gulf of Mexico, Campeche Bank corresponds to the northern extension of the Yucatan Peninsula continental shelf (Fig. 1). Bottoms are sandy, coral and limestone substrates and, to a lesser degree, mud (García and Gómez 1974). Macrobenthos biomass estimates suggest Campeche Bank harbours a great abundance of zoobenthos that is likely to be the dietary basis of various demersal fish species, such as snappers (Spichak and Formoso 1974). All continental freshwater outflows into the sea at Campeche Bank originate from the terrestrial aquifer in the form of point-specific submarine discharges along the Peninsula coast (Aranda-Cirerol et al. 2006). In the northeastern Campeche Bank, in spring and summer, there is a temporary massive upwelling of cold (22.5°C), nutrient-rich water from the depths of the Caribbean Sea which flows east-to-southwest across the continental slope of Campeche Bank (Merino 1997). During the autumn and winter, the region experiences atmospheric cold fronts from the northwest, while in the summer prevailing winds are from the south and southeast, with occasional cyclones during the summer and early autumn (Kornicker and Boyd 1962, Logan 1969). Mean sea surface temperature during the study period fluctuated from 26.8°C in February to 29.3°C in September (Gutiérrez et al. 2021).

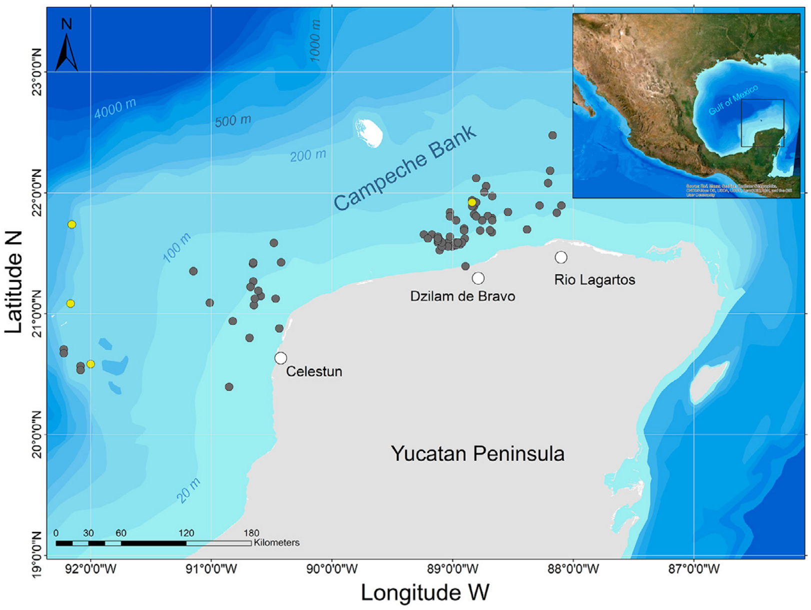

Fig. 1. – Sample sites of *Lutjanus griseus* caught from Campeche Bank, southern Gulf of Mexico, between January 2018 and September 2019. Yellow dots indicate sampling sites where females in actively spawning or past-spawner reproductive subphases were captured.

Sampling and specimen analysis

Specimens were collected monthly between January 2018 and September 2019 in three areas of Campeche Bank near the fishing ports of Celestún (20°52’N, 88°45’W), Dzilam de Bravo (21°30’ N, 88°45’W) and Río Lagartos (21°40’N, 88°10’W) (Fig. 1). The collections were made by fishers from the Mexican artisanal fleet using fibreglass boats (22-26 feet long) equipped with an outboard motor (40 to 150 HP) (Monroy-García et al. 2019). The snappers were caught at 1 to 44 m depth using free diving or hookah harpoon, hook and line, shrimp net and/or cast net (for juveniles). Global positioning system points were recorded for each sampling site.

For each individual, measurements were taken of total length (TL; nearest 0.1 cm), fork length (FL; nearest 0.1 cm), standard length (SL; nearest 0.1 cm), whole-body weight (WW; nearest 1 g), gutted weight (GW; nearest 1 g), and fresh gonad weight (gW; nearest 0.01 g).

In *L. griseus*, oocytes develop homogeneously during the spawning season, regardless of the ovary lobe and lobe zone (Macal-López et al. in press). For histological examination, a sample obtained from the central portion of one lobe from each gonad was preserved in Bouin’s fixative (Gabe 1968) for an average of four days. After fixation, gonad samples were rinsed in 70% ethanol to remove excess fixative, dehydrated in graded ethanol baths (96% and 100%), treated with CitriSolv as an alternative to xylene or benzene, and impregnated in Paraplast baths (melting point: 56°C) following standard histological techniques (Gabe 1968). The blocks containing the samples were sectioned with a microtome (6 µm), and the sections were stained with haematoxylin/eosin (Martoja and Martoja-Pierson 1967).

After sex definition by gonad histological analysis, each female and male was classified into established reproductive phases or subphases (Brown-Peterson et al. 2011): immature, developing (including the early developing subphase), spawning capable (including the actively spawning and past-spawner subphases for females), regressing and regenerating. Males in the actively spawning subphase were identified macroscopically following the criteria of Brown-Peterson et al. (2011). Except for immature individuals, all specimens in any of these phases or subphases were considered sexually mature. All individuals in the spawning capable phase and the actively spawning or past-spawner subphases were considered reproductively active specimens and representative of the mature spawning population (Lowerre-Barbieri et al. 2009).

Size and sex ratio

Size frequency distributions for each sex were established by applying Sturge’s rule (Scherrer 1984) to identify the number and size class interval to be analysed. Median sizes of females and males were compared with the Kruskal-Wallis test. The Kolmogorov-Smirnov test was applied to compare the size frequency distributions of individuals between sexes (Sokal and Rohlf 1997). All statistical analyses were run with the R software (R Core Team 2020) using the FSA library (Mangiafico 2016, Ogle et al. 2021).

Overall and size class sex ratios were calculated considering the number of females per male (F:M). The Pearson chi-square (χ^2) goodness-of-fit statistical test was applied to determine whether the observed sex ratio differed from a balanced sex ratio (1:1) (InfoStat software, Di Rienzo et al. 2014).

Sexual maturity

Minimum size at sexual maturity (L_{min}), corresponding to the smallest adult individual captured during the study was established for both sexes. In snappers, size at maturity increases linearly relative to the maximum size reported for a species or a population (Grimes 1987). The percentage of the maximum size at sexual maturity for females and males was calculated ($L_{min}/L_{max}\times100$), considering L_{max} as the largest individual observed in this population, irrespective of sex. The size at which 50% of individuals reached sexual maturity (L_{50}) was estimated for both sexes using a logistic regression model ($L_{50}=e^{z}\times[1+e^{z}]^{-1}$, where $z=a+b\times\log_{10}FL$), adjusted by the maximum likelihood method (SYTAT 13.1; SYSTAT Software, Inc., San Jose, California). For this analysis, regenerating females were distinguished histologically from immature females by the presence of morphological structures in their ovaries indicative of earlier reproductive activity (i.e. muscle bundle, connective tissue and surrounding blood vessels) (Shapiro et al. 1993, Rhodes and Sadovy 2002). However, this distinction between the two reproductive phases is sometimes uncertain in some species, mainly owing to variability in the time of disappearance from the ovaries of morphological structures indicative of previous reproductive activity (Brown-Peterson et al. 2011, Lowerre-Barbieri et al. 2011). To compensate for this possibility, the reliability of the regenerating and immature female classifications was estimated by comparing median sizes of immature and regenerating females with a Kruskal-Wallis test and their length-frequency distributions using a Kolmogorov-Smirnov test (R Core Team 2020, Mangiafico 2016, Ogle et al. 2021).

Sexual cycle

Sexual cycle was characterized by analysing monthly mean variations in the gonadosomatic index (GSI=100×[gW/GW]) and in the relative proportion of individuals in each reproductive phase or subphase. To run a calendar year analysis, individuals (excluding immatures) were grouped by month of capture.

Presumed *L. griseus* spawning sites on Campeche Bank were identified based on actively spawning female spatial distribution (i.e. ovaries showing oocyte maturation [OM]) or past-spawner subphases (i.e. ovaries showing vitellogenic oocytes and postovulatory follicles) (Fig. 2). The first subphase indicates that females are in an imminent spawning stage, while the second indicates recently past spawning (Brown-Peterson et al. 2011).

Data for TL and SL from previous snapper reproduction studies were converted to FL using the equations FL=0.943×TL+0.157 (r^2=0.984; n=1236) and FL=1.151×SL+0.957 (r^2=0.993; n=1226), based on TL, FL and SL data from the present study.

All measurements are presented as mean±standard error (se), and all statistical analyses were run using an α level of 0.05.

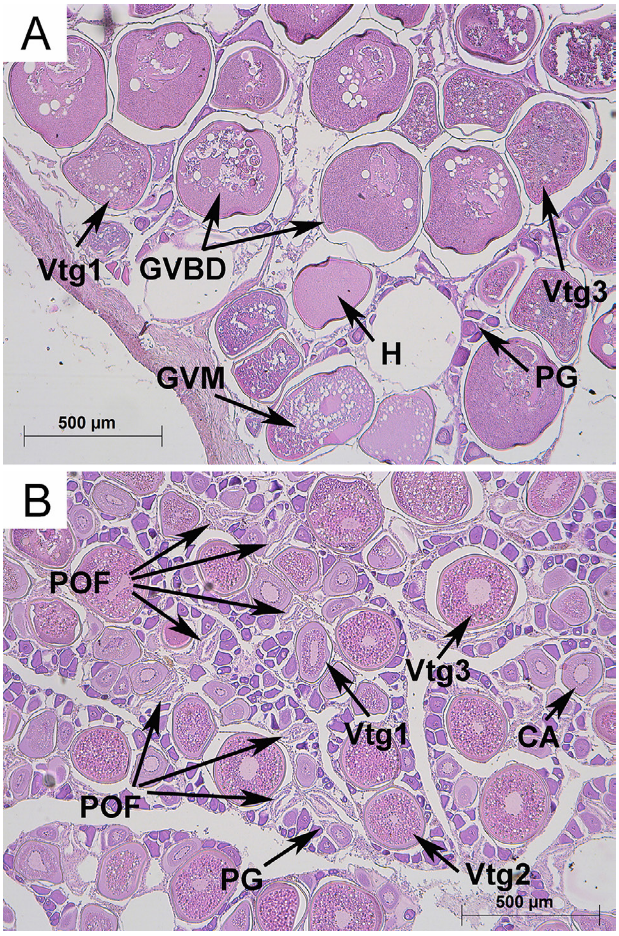

Fig. 2. – Histological sections of ovaries from female *Lutjanus griseus* caught from Campeche Bank, southern Gulf of Mexico, between January 2018 and September 2019. A, actively spawning females; B, past-spawner females. CA, cortico alveolar oocyte; GVBD, germinal vesicle breakdown; GVM, germinal vesicle migration; H, hydrated oocyte; PG, primary growth oocyte; POF, postovulatory follicle; Vtg1, primary vitellogenic oocyte; Vtg2, secondary vitellogenic oocyte; Vtg3, tertiary vitellogenic oocyte (haematoxylin-eosin staining).

RESULTS

Size frequency and sex ratio

A total of 1236 individuals were captured (610 females, 626 males) (Appendix 1). Individual length and weight ranges for sexually mature females (n=322) ranged from 24.2 to 63.9 cm FL (mean=37.2±0.4 cm FL), and 250 to 4248 g WW (mean=917±35 g WW). Sexually mature males (n=544) ranged from 22.8 to 63.2 cm FL (mean=35.5±0.3 cm FL), and 113 to 3876 g WW (mean=794±23 g WW). Length and weight of immature females (n=288) ranged from 14.7 to 46.0 cm FL (mean=30.6±0.4 cm FL) and from 57 to 2906 g WW (mean=522±19 g WW). Immature males (n=82) ranged from 15.5 to 42.5 cm FL (mean=27.5±0.7 cm FL) and from 64 to 1236 g WW (mean=359±24 g WW). Median size did not differ between females (33.2 cm FL) and males (33.3 cm FL) (Kruskal-Wallis test H=0.2224, df=1, P=0.6372), and neither did the size frequency distributions (Kolmogorov-Smirnov test KS=0.069244, P=1.397e-05).

Sex ratio (0.98:1.00) did not differ from a balanced value (1:1) (Pearson =0.16, df=1, P=0.69) (Table 1) and remained balanced regardless of size class. The one exception was the 15 to 20 cm FL size class, in which the sex ratio was biased towards females (2.30:1.00; Pearson =5.12, df=1, P<0.02) (Table 1). No males smaller than 15.5 cm FL were captured (Appendix 1).

Table 1. – Sex ratio by fork length(FL)-class for *Lutjanus griseus* from Campeche Bank, southern Gulf of Mexico. F:M=number of females per male; χ^2, Pearson goodness-of-fit statistic; p, significance value.*: significant differences from a ratio of 1:1.

FL-class (cm)	Number		Sex ratio (F:M)	χ^2 value	p
	Females	Males			
10.1 – 15.0	1	0	-	-	-
15.1 – 20.0	23	10	2.30:1.00	5.120	0.0236*
20.1 – 25.0	29	34	0.85: 1.00	0.400	0.5287
25.1 – 30.0	144	162	0.89: 1.00	1.060	0.3035
30.1 – 35.0	163	154	1.06: 1.00	0.260	0.6132
35.1 – 40.0	125	124	1.01: 1.00	0.004	0.9405
40.1 – 45.0	74	92	0.80: 1.00	1.950	0.1624
45.1 – 50.0	31	31	1.00: 1.00	0.000	0.9999
50.1 – 55.0	12	11	1.09: 1.00	0.040	0.8348
55.1 – 60.0	5	7	0.71: 1.00	0.330	0.5637
60.1 – 65.0	3	1	3.00: 1.00	1.000	0.3173
Total	610	626	0.97: 1.00	0.210	0.6490

Sexual maturity

The L_{min} was 24.2 cm FL for sexually mature females (individual in regeneration phase), and 22.8 cm FL for sexually mature males (individual in regression phase). The L_{max} recorded for *L. griseus* on Campeche Bank was 63.9 cm FL for females and 63.2 cm FL for males; therefore, the percentage of maximum size at which females reached maturity was 38% and that for males was 36%. For females, L_{50} was 32.2 cm FL (31.0-33.5 cm FL limits, 95% confidence interval) and for males it was 22.0 cm FL (20.0-23.6 cm FL limits, 95% confidence interval) (Fig. 3).

Median sizes of immature females (30.3 cm FL) were significantly lower than median sizes of regenerating females (36.6 cm FL) (Kruskal-Wallis test H=94.91, df=1, P<2.2e-16). The length-frequency distribution of immature females differed from that of regenerating females (Kolmogorov-Smirnov test KS=0.0617, P=0.0355) (Fig. 4). These results confirm the accuracy of discrimination between immature and regenerating females based on ovary histology in the present study.

Sexual cycle

Monthly evolution of the GSI for females and males throughout a calendar year showed that reproductive activity in *L. griseus* begins in May and ends in September (Fig. 5). Maximum mean GSI values were observed in June for males (1.01±0.14%) and in August for females (1.38±0.34%). The low mean GSI values observed between October and April for both females (0.33±0.02% and 0.46±0.05%, respectively) and males (0.13±0.01% and 0.12±0.01%, respectively) indicate that they were reproductively inactive during this period.

Annual monthly variation in the percentage of individuals in different reproductive phases and subphases confirmed the GSI analysis observations (Fig. 6). Re-

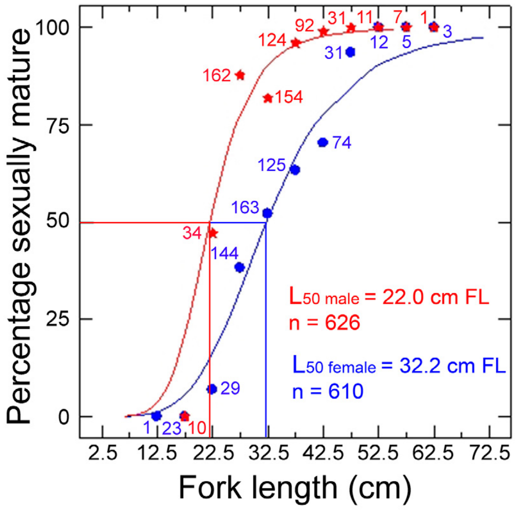

Fig. 3. – Percentage in relation to fork length of sexually mature female and male *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019. The proportion of sexually mature fish within each size class was plotted using a binary logistic regression. Vertical lines indicate the length at which 50% of individuals were mature (L_{50}). Numbers indicate sample size for each size class. Sexually mature fish are early developing, developing, spawning capable, actively spawning, past-spawner (only for females), regressing and regenerating individuals.

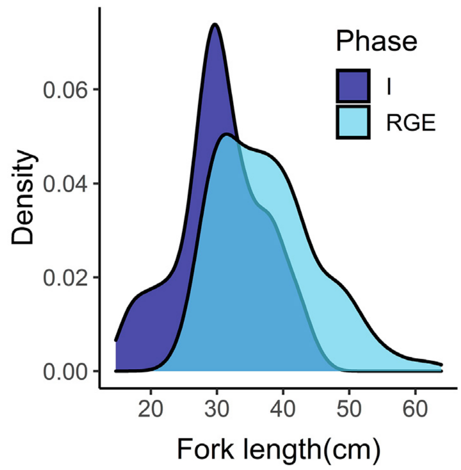

Fig. 4. – Size-frequency distributions for immature (I) and regenerating (RGE) female *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019.

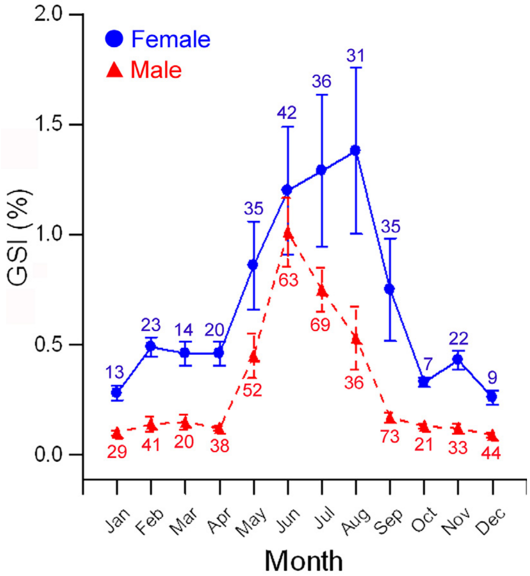

Fig. 5. – Seasonal variation of the Gonadosomatic index (GSI; mean±se) for female and male *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019. Numbers indicate sample size for each pooled sampled month.

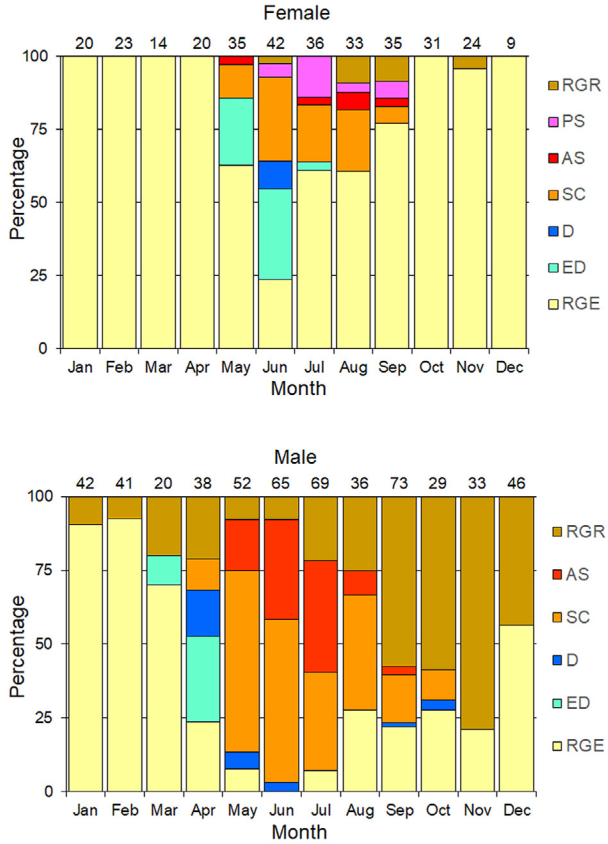

Fig. 6. – Seasonal variation of the percent frequency of female and male *Lutjanus griseus* caught from Campeche Bank in the southern Gulf of Mexico between January 2018 and September 2019, classified according to reproductive phases and subphases over a single year (RGE, regenerating; ED, early developing; D, developing; SC, spawning capable; AS, actively spawning; PS, past-spawner; RGR, regressing). Numbers indicate sample size for each pooled sampled month.

productively active females (n=47; 15% of captured females) were observed between May and September and reached a maximum percentage of captures in July (36%; n=13). The highest percentage of spawning capable females was recorded in June (29%; n=12), that for actively spawning females in August (6%; n=2), and that for past-spawning females in July (14%; n=5). From May to September, regenerating females represented between 24% and 77% of females captured monthly. Few regressing females were observed in monthly captures (range: 2-9%; n=1-3). Between October and April, all or most (96% in November) captured females were in the regenerating phase. Although males were reproductively active during a slightly longer time than females (April to October), their seasonal peak in reproductive activity was very similar to that of females (Fig. 6). The highest percentages of spawning capable and actively spawning males were observed between May and August (range=47-89%; n=17-58). The highest percentages of actively spawning males were observed in June (34%; n=22) and July (38%; n=26). The percentages of regenerating males were lowest between May and August (range=0-28%; n=0-10) and highest between December and March (range=57-93%; n=26-38).

DISCUSSION

The use of different fishing gears to capture *L. griseus* specimens on Campeche Bank generated a sample consisting of individuals distributed over a wide range of representative lengths (14.7-63.9 cm FL). This snapper species is reported to reach a maximum size of 89 cm TL (=84 cm FL), although the most frequent size is 40 cm TL (=38 cm FL) (Allen 1985). However, in this study juveniles smaller than 14.0 cm FL were not collected, probably because the fishing area covered by the artisanal fleet in Yucatan excludes estuaries, coastal lagoons and the coastal margin, which are nursery habitats for *L. griseus* (Starck 1971, Claro and Lindeman 2004, Faunce and Seafy 2007). The median sizes and length-frequency distributions for both sexes on Campeche Bank were identical, as previously reported for *L. griseus* populations in Florida (Starck 1971, Domeier et al. 1996). According to Domeier et al. (1996), this demographic trait could result from this species's gonochoric-type sexuality pattern.

Grimes (1987) states that snappers can exhibit a slightly female-biased sex ratio in larger size classes because of differences in growth and mortality between sexes. Moreover, the overall sex ratio in *L. griseus* populations frequently favours females, as reported in the west Florida Keys (Domeier et al. 1996), Cuba (Báez et al. 1982, Claro 1983) and Venezuela (Guerra-Campos and Bashirullah 1975) (Table 2). However, the sex ratio observed here in the Campeche Bank population was balanced, as previously observed in populations in the Everglades National Park and the Florida Keys (Croker 1962, Starck 1971), the west coast of Florida (Allman and Goetz 2009) and the coast of Guatemala (Andrade and Santos 2019) (Table 2). Interpopulational variation

Table 2. – Fork length (FL) at maturity, sex ratio and reproductive season reported for *Lutjanus griseus* populations from the Gulf of Mexico and the Caribbean Sea (F, female; M, male; L_{min}, minimum size at which individuals became sexually mature; L_{max}, maximum size observed in the sample; L_{min}/L_{max}, length at first maturity expressed as a percentage of maximum length; L_{50}, length at which 50% of individuals were mature). [a], standard length (SL, cm) data converted to FL (cm) using the formula FL=0.957+1.151×SL (r^2=0.993, n=1226), calculated from data of the present study. [b], total length (SL, cm) data converted to FL (cm) using the formula FL=0.157+0.943×TL (r^2=0.984, n=1236), calculated from data of the present study. [c], pooled sex data. [d], more accurate estimate of maturity. [e], peak spawning.

	Fork length (cm) at maturity						
Sex	L_{min}	L_{max}	L_{min}/L_{max}×100 (%)	L_{50}	Sex ratio F:M	Reproductive season	Reference
				United States (Florida)			
-	-	-	-	-	1.10:1.00	-	Croker (1962)
F	23.4[a]	57.2[a]	40.9	-	0.87:1.00	Apr-Sept (Jun-Aug)[e]	Starck (1971)
M	22.3[a]		40.0	-			
F	23.7[a]	58.2[a]	40.7	-	1.20:1.00	May-Sept (Jun-Aug)[e]	Domeier et al. (1996)
M	21.9[a]		37.6	-			
	-	--	-	-	-	May-Sept (Jul)[e]	Allman and Grimes (2002)
-	-	-	-	-	1:00:0.99	-	Allman and Goetz (2009)
-	-	-	-	23.9-28.8 30.0[d]	1.00:1.00	-	SEDAR (2018)
				Mexico (Yucatan)			
F	24.2	63.9	37.9	32.2	0.97:1.00	May-Sept (Jun; Aug)[e]	Present study
M	22.8		35.7	22.0			
				Cuba			
F	24.6	53.0	46.4	-	1.58:1.00	Jun-Sept (Jul-Aug)[e]	Báez et al. (1982)
M	22.9		43.2	-			
F	21.0	51.0	41.2	-	1.30:1.00	Jun-Sept (Jul-Aug)[e]	Claro (1983)
M	18.0		35.3	-			
				Guatemala			
F	26.1[b]	52.0[b]	50.2	29.4[b, c]	1.00:1.00	Apr-Sept (Jun-Jul)[e]	Andrade and Santos (2019)
M	19.6[b]		37.7				
				Venezuela (Isla de Cubagua)			
-	-	62.4[b]	-	-	1.96:1.00	Apr-Sept (Jun-Jul)[e]	Guerra-Campos and Bashirullah (1975)

in sex ratio in *L. griseus* may occur in response to certain spatial-temporal factors such as habitat type and climatic season (Claro and Lindeman 2004).

On Campeche Bank, male *L. griseus* reach sexual maturity at a smaller size than females, as reported for other populations (Table 2). The percentages of maximum size at sexual maturity in females (38%) and males (36%) show that the Campeche Bank population exhibits a typical maturity pattern for snapper populations distributed on continental shelves or in shallow waters (mature at about 41% and 43% of maximum size, respectively), as defined by Grimes (1987). Similar results have been reported for Florida continental shelf populations: 40% for females and 37% to 38% for males (Starck 1971, Domeier et al. 1996). On the Guatemalan coast, however, the maximum size at sexual maturity percentage for *L. griseus* was higher in females (50%) than in males (38%) (Table 2); the female value was similar to those established by Grimes (1987) for snapper populations in insular or deep-water regions (mature at about 51% and 49% of maximum size, respectively). In Cuba, by contrast, the maximum size at sexual maturity percentages reported for *L. griseus* females (41%-46%) and males (35%-43%) were more typical of species and populations distributed on continental shelves (Báez et al. 1982, Claro 1983) (Table 2). Differences between observed values and those proposed by Grimes (1987) may be explained by errors in calculating L_{min} in females and males and/or L_{max} for the studied populations. For example, Báez et al. (1982), Claro (1983) and Andrade and Santos (2019) calculated L_{min} for both sexes by macroscopic examination of gonads, which is considered the least accurate method (Murua et al. 2003, Lowerre-Barbieri et al. 2011). The L_{max} values reported by these authors were lower (51-53 cm FL and 55 cm TL [=52 cm FL]) than the L_{max} observed in the present study. Another possible explanation for discrepancies is that Grimes's

(1987) proposed values are not generally applicable to all snapper species and populations. For example, populations of lane snapper *Lutjanus synagris* (Linnaeus, 1758) from Cuba, Puerto Rico, Jamaica and Trinidad have an atypical sexual maturity pattern characteristic of continental shelf areas, while the population off Venezuela has an atypical pattern characteristic of island regions (Trejo-Martínez et al. 2021).

Two previous reports containing L_{50} data for *L. griseus* are for the populations of the northern Gulf of Mexico (SEDAR 2018) and off the Guatemalan coast (Andrade and Santos 2019) (Table 2). For the northern Gulf of Mexico population, the more recent calculation of female length at 50% maturity is between 23.9 and 28.8 cm FL, with 90% of individuals being mature at 36.2 cm FL. However, if based on female GSI values, a significant contribution to the spawning stock is not achieved until 30.0 cm FL, a size considered a more accurate estimate of L_{50} for *L. griseus* (SEDAR, 2018). Combining data from both sexes, Andrade and Santos (2019) estimated an L_{50} of 31.1 cm TL (=29.5 cm FL) for the Guatemalan population. The values from both studies are between those observed for females and males in the present study. In contrast, a study of *L. griseus* off Florida over 25 years ago found that 90% of individuals (females and males combined) were mature at 20 cm SL (=24 cm FL) and 100% at 24 cm SL (=29 cm) (Domeier et al. 1996). Compared with the L_{50} data values reported for the northern Gulf of Mexico (SEDAR 2018) and Guatemala (Andrade and Santos 2019), and those in the present study, these values seem to be serious underestimates and are difficult to explain. Perhaps the number of specimens analysed by Domeier et al. (1996) by means of histological preparation of gonads was too small (n=122), and/or mistakes were made in identification of the microscopic stages of gonadal maturation.

Spawning season for the Campeche Bank *L. griseus* population occurs from May to September, with probable spawning pulses between June and August, which are typical of snapper species and populations from continental shelves (Grimes 1987). These results coincide with those for *L. griseus* populations from other continental shelf regions such as Florida (Starck 1971, Domeier et al. 1996, Allman and Grimes 2002) and Guatemala (Andrade and Santos 2019) (Table 2). However, *L. griseus* populations from insular regions such as Cuba (Báez et al. 1982, Claro 1983) and Cubagua Island in Venezuela (Guerra-Campos and Bashirullah 1975) also display a restricted spawning season centred in summer, a spawning season pattern characteristic of continental shelf populations (Table 2). Thus, as previously noted by Grimes (1987), insular *L. griseus* populations do not always exhibit reproductive seasons strictly in accordance with their habitat type.

Collection sites for two of the actively spawning females (n_{total}=6) and three of the past-spawner females (n_{total}=10) analysed in the present study could not be placed confidently. But it is known that the others (four actively spawning and seven past-spawner females) were caught at three collection sites west of Celestún (range=29-44 m deep) and one north of Dzilam de Bravo (22 m deep), suggesting that these may be *L. griseus* spawning areas. Actively spawning and past-spawner females were captured within seven days before and two days after the full moon phase. Only one actively spawning female was caught five days after the new moon. This would coincide with a report that in Cuba *L. griseus* spawners migrate to waters 20 to 30 m deep to reproduce at night near the full moon (Claro 1983, Claro and Lindeman 2003). Larger movements by grey snapper are related to spawning migration and it is probable that this species aggregates at offshore spawning sites (SEDAR 2018). However, *L. griseus* spawning aggregations have not yet been fully validated (Domeier and Colin 1997, Lindeman et al. 2000; Binder et al. 2021). The Campeche Bank *L. griseus* population exhibits an asynchronous ovarian organization and is a batch spawner (Macal-López et al. in press). However, spawning frequency/spawning interval was not calculated in this study because there were insufficient numbers of reproductively active females in the sample. In the northern Gulf of Mexico, it has been estimated that the *L. griseus* spawning season is 137 days long and encompasses 37 spawns within that period (SEDAR 2018). Using these values provides an estimated spawning interval of 3.7 days for this snapper.

Despite a paucity of reproductively active females, particularly those in the active spawning and past-spawner subphases, the present data were sufficient to characterize sexual maturity and spawning season for *L. griseus* on Campeche Bank. This is an ongoing challenge in the study of *L. griseus* (Starck 1971, Rutherford et al. 1983, Domeier et al. 1996), because maturing adults migrate from shallow coastal waters to spawning grounds in deeper reef areas during the spawning season (Starck, 1971, Domeier et al. 1996, SEDAR 2018). Collection for the present study was done mainly in shallow waters, which may have caused the scarcity of reproductively active females in the collections. However, high percentages of reproductively active males (range=19%-89%), including various in the actively spawning subphase (range=3%-38%), were caught every month of the spawning season (May-September). Mature *L. griseus* decrease feeding activity during the spawning season (Claro 1983), and thus reproductively active females may have been less accessible than males to the fishing gear used during the spawning season, especially to passive techniques such as hook and line. Another possible explanation is that most reproductively active females start migrating to offshore spawning grounds earlier in the season than reproductively active males, and/or that most reproductively active males make continuous movements during the spawning season between offshore spawning sites and inshore feeding sites

The present results for the Campeche Bank *L. griseus* population corroborate Grimes's (1987) concept regarding continental reproductive pattern in snappers. For this continental population, sexual maturation occurred at a smaller size in males than in females, and between 36% and 38% of the maximum size for both sexes. The spawning season was centred around summer, with spawning peaks observed between June and

August. This study generates new data on core aspects of the reproductive strategy of *L. griseus*, one of the least-studied snappers in the western Central Atlantic. It expands knowledge on the life history of a species vital to tropical marine ecosystem ecology and provides data fundamental to stock assessment and to defining the fisheries management policies most appropriate to specific snapper populations.

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APPENDIX

Appendix 1 – Sex, number of individuals (n), mean±se, and range of fork length and whole-body weight of *Lutjanus griseus* sampled between January 2018 and September 2019 on Campeche Bank, southern Gulf of Mexico.

		Female				Male				
		Fork length (cm)		Whole-body weight (g)			Fork length (cm)		Whole-body weight (g)	
Month	n	Mean	Range	Mean	Range	n	Mean	Range	Mean	Range
January	36	38.7±0.9	27.4-50.6	948±68	348-2100	46	40.9±1.0	27.2-56.6	1115±87	116-2701
February	41	39.4±1.8	20.1-63.9	1182±146	132-4248	53	41.6±1.4	17.4-59.3	1311±110	85-3081
March	55	29.7±1.1	16.9-46.6	500±51	80-1562	44	29.7±1.3	16.5-46.4	504±61	76-1703
April	41	32.6±1.8	14.7-56.7	746±105	57-3146	46	33.6±1.2	15.5-51.0	701±59	64-1931
May	51	36.0±0.9	19.7-53.2	875±85	123-2906	52	34.7±0.7	24.8-45.5	693±45	260-1727
June	74	32.4±0.6	21.9-45.4	584±35	167-1537	66	32.0±0.7	21.2-45.6	567±41	154-1799
July	61	34.2±0.8	22.5-51.2	681±51	205-2118	71	34.7±0.7	22.8-52.5	718±50	194-2145
August	46	34.4±0.6	27.5-46.9	670±38	323-1644	36	35.5±0.9	26.5-49.7	747±61	282-1888
September	66	33.7±0.7	25.5-52.0	677±46	240-2042	75	33.1±0.6	23.6-47.1	618±34	113-1666
October	58	31.9±0.6	19.0-43.6	541±35	116-1428	56	32.0±0.6	26.0-48.4	545±39	291-1778
November	44	40.7±1.3	29.1-61.0	1246±126	391-3489	34	40.3±1.3	29.0-63.2	1191±124	402-3876
December	37	28.4±0.4	23.0-36.4	375±16	235-765	47	28.1±0.5	23.5-37.7	375±22	210-936
Total	610	34.1±0.3	14.7-63.9	730±22	57-4248	626	34.4±0.3	15.5-63.2	737±21	64-3876