

Research Article

Reproductive season and first maturity size of the spotted rose snapper *Lutjanus guttatus* (Steindachner, 1869) in the Pacific of Guatemala: A baseline for fishery management

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ABSTRACT. The spotted rose snapper (*Lutjanus guttatus*) is a commercially important species that provides economic income to small-scale fisheries in the Pacific coastal regions of Guatemala; however, there are no studies on this species that establish a baseline of knowledge on their reproductive aspects and potential management measures. The present study was carried out to obtain the first knowledge on the reproductive behavior of this resource, which will contribute to the establishment of future management strategies for the fisheries. Aspects of gonadal-maturity phases and reproductive indicators such as the condition factor, gonadosomatic index, and temporal oocyte diameter were analyzed to estimate reproductive development and the size at first maturity. The results suggest that the spotted rose snapper has two well-defined reproductive periods - from October to December and March to May. These periods were closely related to temperatures that ranged from 29 to 31°C. In addition, according to the monthly monitoring of the oocyte diameter density distribution, it is suggested that spotted rose snapper in the region could participate in up to three spawning events during the reproductive season, with gamete development occurring throughout most of the entire study period. The first size at maturity was a total length (TL) of 33.49 cm (confidence interval = 30.95-36.14 cm). This information is important for sustainable fishery management and provides a baseline for future research.

Keywords: *Lutjanus guttatus*; reproductive period; size at first maturity; sustainable fishing; management strategies; Pacific of Guatemala

INTRODUCTION

The Pacific coast of Guatemala is of great economic importance, with more than 1,500 fishers directly dependent on exploited marine fish species for their income and livelihood (DIPESCA/MAGA 2018,

Hernández-Padilla et al. 2020). Despite this, there is a lack of historical information on landings and fishing efforts that could contribute to the sustainable management and control of fisheries in the region. The spotted rose snapper (*Lutjanus guttatus*) fishery in the Guatemalan Pacific is considered commercially impor-

tant due to its high demand in local, regional, and export markets (Andrade et al. 2023). The resource is exploited by both the industrial and the small-scale fleets. The fishery mainly comprises two species, the spotted rose snapper, and the Colorado snapper (*L. colorado*), representing 68 and 32% of the total catch, respectively (Mendoza-Arzu 2018). Despite this, no management scheme regulates the catch of these resources in the region or protects reproductive events. Knowledge of reproductive parameters is fundamental to determining appropriate fishery management measures (Marshall 2009, Kjesbu 2016).

The reproductive period of Lutjanidae seems to be correlated with several environmental factors, including temperature and photoperiod, although it also seems to coincide with spring tides (Russell & McDougall 2008, Piñón et al. 2009, SAGARPA 2013, Lowerre-Barbieri et al. 2015, Fernandes et al. 2022). The reproductive seasonality serves the purpose of maintaining the survival of the greatest number of larvae, therefore achieving recruitment success, which is an essential parameter for the sustainability of the fisheries (Boza-Abarca 2003, Lowerre-Barbieri et al. 2017, Somarakis et al. 2019). Temperature increase can disturb the aromatase synthesis or activity, affecting the reproductive cycle and potentially causing mistiming or discontinuity in spawning seasonality. This alteration could lead to a skewed sex ratio favoring males and a consequent reduction in population fecundity (Brule et al. 2022). These factors are often related to the timing of final maturation (Boza-Abarca 2003). The reproductive cycles aim to maximize the survival of larvae, thereby achieving recruitment success, which is an essential parameter for the sustainability of fishery exploitation (Boza-Abarca 2003, Lowerre-Barbieri et al. 2017, Somarakis et al. 2019).

There are several studies on the reproductive cycles of different species of lutjanids (Cruz-Romero et al. 1996, Arellano-Martínez et al. 2001, White & Palmer 2004, Oliveira-Freitas et al. 2014). Research has been conducted on the spotted rose snapper in some areas of the Pacific, where it has been highlighted that this species reproduces throughout the year with variation in the reproductive peaks according to the geographical area. In the Colombian Pacific, it has been reported that the highest reproductive activity occurs in June and from September to October (Correa-Herrera & Jiménez-Segura 2013), and in Costa Rica, it occurs in March and September (Soto-Rojas et al. 2009). The highest reproductive activity has been reported between March and April and August and November in Guerrero, Mexico (Arellano-Martínez et al. 2001),

from July to October in Colima, Mexico (Cruz-Romero et al. 1996), and from June to September in Nayarit, Mexico (Lucano-Ramírez et al. 2023). Generally, environmental factors determine the presence and duration of the reproductive cycles in these marine organisms (Carter & Perrinee 1994), so it is expected that the seasonality of the reproductive cycle varies according to the geographical area. In this sense, it is important to determine the reproductive aspects of *L. guttatus* in areas of exploitation in Pacific Guatemala as a baseline for establishing a fishery management scheme that regulates the exploitation of spotted rose snapper during the most important reproductive events.

MATERIALS AND METHODS

Fieldwork

The study area is located in the Pacific of Guatemala, where an average of 18 individuals (± 3.6) were randomly selected and recorded monthly from the commercial catch of small-scale fisheries at the landing ports of Buena Vista Iztapa and Puerto de San José from October 2017 to June 2018 (Fig. 1). Due to weather conditions, it was not possible to collect samples from July through September. Total weight ($TW \pm 0.001$ g) and total length ($TL \pm 0.1$ cm) were recorded. The fish were then dissected to extract the gonads, which were weighed (gonad weight, $GW \pm 0.001$ g), fixed in 10% formaldehyde for 48 h, washed, and then preserved in 70% alcohol for transport.

The gonads were taken to the Marine Invertebrate Laboratory of the Interdisciplinary Center of Marine Sciences (CICIMAR, by its Spanish acronym) of the National Polytechnic Institute in La Paz, Mexico, where they were processed using the histological method of kerosene embedding and hematoxylin-eosin staining (Humason 1979). Once the slides were mounted, they were observed under the microscope, and images were taken. In this way, the sexes were differentiated, and the stages of gonadal development and oocyte type were described based on what was proposed by Santamaría-Miranda et al. (2003) and Lucano-Ramírez et al. (2023). On this basis, the reproductive cycle of the species was established.

Oocyte diameter

As a quantitative measure, oocyte diameter was measured monthly by selecting five slides per month. The oocytes were measured using the SigmaScan[®] Pro version 5 program, and the largest and smallest diameters of approximately 50 oocytes from each preparation were measured and averaged, selecting

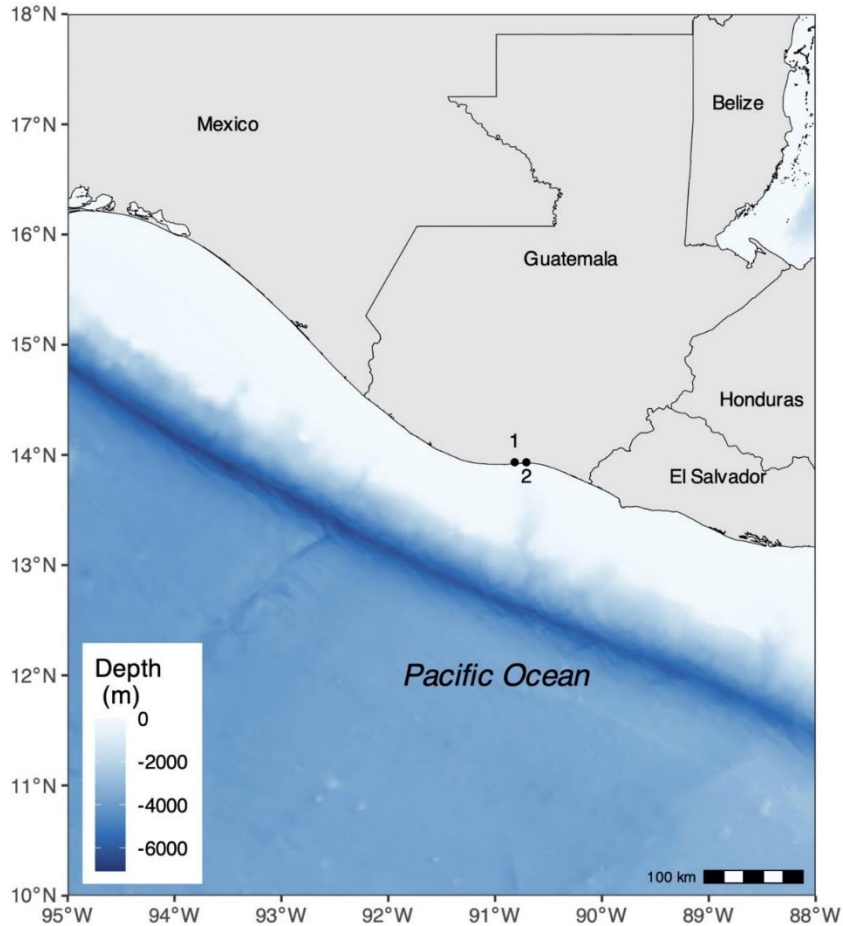


Figure 1. Location of the study area on the Pacific coast of Guatemala: 1: Puerto San José, and 2: Puerto Buena Vista Iztapa.

only those that presented the nucleolus. Oocyte diameter was estimated by the resulting average from the greatest and smallest axis diameter (Lucano-Ramírez et al. 2014). The data obtained were used to construct the monthly relative frequency of oocyte diameter. Density plots were created to evaluate the monthly distribution of the diameter of the oocytes with the help of the *ggridges* package (Wilke 2024) of the R programming language (R Core Team 2024).

Sex ratio

The monthly and total sex ratios were evaluated using a hypothesis test from χ^2 against the null hypothesis of one female to one male with a significance level of $P = 0.05$ (Sokal & Rohlf 1995).

Total length (TL) - total weight (TW) relationship and condition factor

The relationship between TL and TW was analyzed using the potential equation $TW = aTL^b$ (Ricker 1975).

The equation was fitted to the observed data to obtain the model parameters a and b through a nonlinear fit using the *nls* function of the R programming language (R Core Team 2024). The condition factor (K) indicates each individual's physiological state, so it was estimated with the equation $K = TW/TL^b \times 10$, where b is the parameter resulting from the TL-TW relationship (Bagenal & Tesch 1978).

Gonadosomatic index

The gonadosomatic index (GSI) was determined with the data obtained from TW and GW. The GSI was calculated with the following equation (Arellano-Martínez et al. 2001):

$$GSI = \frac{GW}{TW} \times 100$$

A cross-correlation test was used to determine the similarity between K and the GSI over time, with time lags starting at one month.

Total length at first maturity

Length at first maturity ($TL_{50\%}$) was defined as the length at which 50% of the individuals were mature (maturity and spawning phases). This length was estimated by fitting a logistic model to the observed data using the following equation:

$$P_i = \frac{1}{1 + e^{-\frac{(TL_i - TL_{50\%})}{\alpha}}}$$

where P_i is the proportion of mature organisms (in mature and spawning phases) in the i -th TL interval, TL_i is the mean class of the i -th TL interval, and α is the intercept (Brouwer & Griffiths 2005). The logistic curve was fitted to the observed data by minimizing the negative value of the following binomial log-likelihood function:

$$-\sum_{i=1}^n [m_i \times \ln(P_i) + (n_i - m_i) \times \ln(1 - P_i)]$$

where n_i is the total number of organisms in the i -th TL interval, and m_i is the number of mature organisms in the i -th TL interval.

Environmental variables

Monthly temperature composition data for the study area were obtained from satellite imagery in the Ocean Color NASA database (<https://oceancolor.gsfc.nasa.gov/>). The images obtained had a resolution of 4×4 km. The images were downloaded in HDF format and displayed using the R programming language's raster package (Hijmans 2023, R Core Team 2024). Monthly fluvial precipitation and photoperiod records were also obtained. Photoperiod information was downloaded from the US Naval Observatory website (<https://aa.usno.navy.mil/>). On the other hand, the fluvial precipitation was obtained from the website of the National Institute of Statistics of Guatemala (<https://www.ine.gob.gt/estadisticas/bases-de-datos/estadisticas-ambientales/>).

An exploratory analysis was performed to determine if there was a trend in the GSI concerning the environmental variables, and it was found that only temperature showed a trend. A Gaussian model was used to model this trend, fitted with the nls function of the R programming language (R Core Team 2024). The Gaussian model has the characteristic that it has two parameters, the mean (μ) and the deviation from the mean (σ) (Sokal & Rohlf 1995). This model made it possible to estimate the average GSI value for all months, including those without data.

RESULTS

A total of 179 individuals were analyzed, of which 87 were males and 92 were females. The χ^2 test showed no statistically different monthly number of males and females. Therefore, the sex ratio was not different from 1:1 throughout the sampling period. The length of the captured individuals ranged from 18.0 to 53.2 cm TL for males and from 19.5 to 50.9 cm TL for females.

Description of the stages of gonadal development

Five stages of gonadal development have been identified in females (immature, developing, developed, mature, and spawning), while only three have been identified in males (immature, developed, and ejaculation). Their characteristics are described below:

Immature gonad

The first stage of maturation is in both sexes. In females, it is evident that the lamellae are thin and contain ovogonia or oocytes of nucleolar chromatin (NC) type or initial growth. The latter are very small cells, although of variable size, with an average diameter of $50.7 \pm 13.7 \mu\text{m}$. These tend to be polygonal in shape with rounded angles, deep purple cytoplasm (basophilic) without yolk, and the nucleus is light pink with multiple nucleoli at the periphery. Similarly, oocytes perinuclear (OPN) are observed, which are mainly oval with purple cytoplasm, are not as deep as NC, have no vitellus, and have a pink nucleus ($90 \pm 22.7 \mu\text{m}$) with deep purple nucleoli (Fig. 2a). In males, the immature gonad can be identified primarily by the beginning of the spermatogenesis process, characterized by the abundance of spermatogonia and spermatocytes growing inside the seminiferous vessels, giving them a compact appearance; spermatozoa are also present in the asinine lumen, but in a very low proportion concerning the rest of the cells (Fig. 2f). This phase was present in all sampling months but was more frequent (<40%) in January and February.

Developing gonad

This phase was present only in females. NC and OPN oocytes are observed and are characterized by the presence, although in smaller quantities, of cortical alveolar oocytes (CA). These are medium-sized cells with an average diameter of $150 \pm 28.3 \mu\text{m}$. They have oval and round shapes, and their main characteristic is the presence of round vitelline vesicles in the cytoplasm, which surrounds the nucleus. The cytoplasm is light magenta with a light pink nucleus. It is possible to observe some vitellogenin oocytes (VO),

which are large cells with an average diameter of $275 \pm 47 \mu\text{m}$. Although they are irregular in circumference, they are oval and magenta. The vitellus appears in greater proportion as distinct stripes in the cytoplasm (Fig. 2b). This stage was present in only five of the seven sampling months, with the highest frequency in November and December (21 and 26%, respectively).

Developed gonad

In females, this phase is observed with similar characteristics to the previous phase described; however, the proportion of immature cells (OPN:NC) is lower, and the proportion of VO increases (Fig. 2c). In males, many spermatozoa are observed in the lumen of the acini, although the process of spermatogenesis continues in the walls of the acini, the amount of spermatogonia and spermatocytes decreases (Fig. 2g). This phase was absent in February. However, the other sampling months maintained high frequencies, up to 54.5% in October.

Mature gonad

In the mature gonad, in addition to the oocytes of the migratory nucleus (MN), VO appear at a higher density than in the previous phase. These oocytes reach the largest size with an average diameter of $427 \pm 33 \mu\text{m}$. They have irregular shapes, and their main characteristic is large vesicles of yolk that occupy almost all of the space of their cytoplasm, which is why they lack coloration. Their nucleus is no longer concentric, while the oocytes of earlier stages appear in smaller numbers (Fig. 2c). This phase is very unstable, i.e. the gametes can be expelled very easily, so it does not occur in males. The months in which this phase was observed were October, February, and March, with a frequency of less than 13%.

Spawning/ejaculating gonad

In females, large empty spaces are usually occupied by hydrated oocytes. During this period, the presence of VO and MN continues, and hydrated oocytes also appear. Although they have a mean diameter of $297.8 \pm 59.8 \mu\text{m}$, they are characterized by a variable shape and are acidophilic, and postovulatory follicles (Fig. 2d) are present at this stage. In males, large empty spaces are observed in the lumen of the gonad, and only dense patches of spermatozoa are of a deep acidophilic color. Evidence of a possible onset of the gonadal cycle was observed in the periphery of the gonad (Fig. 2h). This phase was observed in all sampling months, with a higher frequency from April to June (<40%).

Condition factor (*K*) and gonadosomatic index (GSI)

Both *K* and the GSI showed significant variations during the study period. Initially, no direct correlation was observed between the two indices, so a cross-correlation was carried out, with *K* decreasing monthly. The highest correlation was obtained with a two-month difference between the two indices ($r = 0.47$) (Fig. 3a). The GSI values were consistent with the reproductive period described in Figure 3c. At the same time, the *K* showed that the condition decreased after the first reproductive peak and did not recover until after the second reproductive peak.

Environmental factors

A Gaussian model explained a correlation in the exploratory analysis of monthly mean sea temperature and monthly GSI. No trend was found in the photoperiod and precipitation, so they were excluded from the analysis. Figure 3b shows that the temperatures where the highest GSI values are obtained range from 29 to 31°C, suggesting that these conditions favor the maturation and spawning/ejaculation processes of individuals.

With the Gaussian model, the average value of the monthly GSI was predicted for an entire type year, suggesting two reproductive periods - one from October to December and the second from March to May, with a spike in June (Fig. 3b). The low temperatures coincided with the peak of the percentage of immature fish, confirmed by the maturation phases classified by histological analysis of the gonads.

Monthly analysis of oocyte diameter

A modal group of oocytes smaller than 130 μm was present during all months, indicating constant oocyte production throughout the study period (Fig. 4). In October, November, and December, up to three modal groups of oocytes with cells reaching up to 420 μm was observed, coinciding with a reproductive peak recorded (Fig. 3c). In addition, up to three modal groups were observed during the February to June period (Fig. 4).

First maturity size

Mature individuals were found in the range of 19.5 to 50.9 cm TL. The TL at which 50% of the mature spotted rose snapper individuals of both sexes showed maturity was 33.49 cm (confidence interval = 30.95-36.14 cm) (Fig. 5).

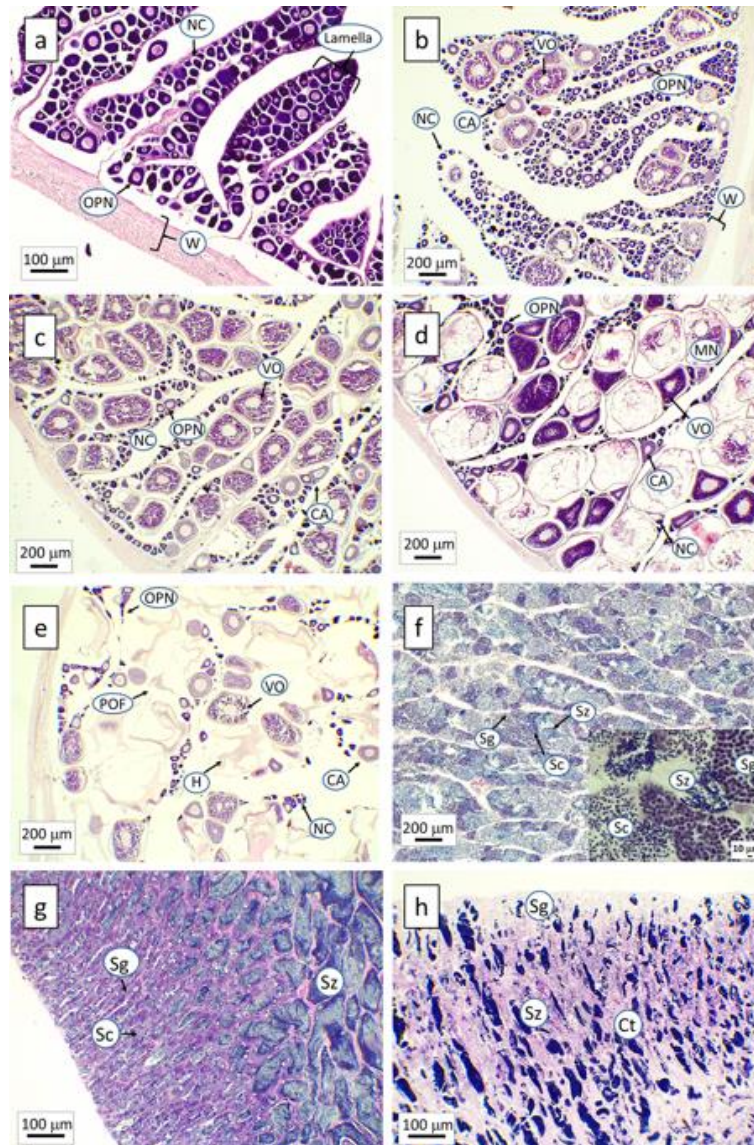


Figure 2. Stages of gonadal development in the spotted rose snapper, *L. guttatus*. a-e) Females; a) immature gonad, b) developing gonad, c) developed gonad, d) mature gonad, e) spawning gonad. f-h) Males; f) immature gonad, g) developing gonad, h) ejaculating gonad. NC: oocyte nucleolar chromatin, OPN: oocyte perinuclear, CA: cortical alveolar oocytes, VO: vitellogenin oocytes, MN: migratory nucleus oocytes, H: hydrated oocytes, W: gonadal wall. Hematoxylin-Eosin Technique POF: postovulatory follicles, Sg: spermatogonia, Sc: spermatocytes, Sz: spermatozooids, Ct: conjunctive tissue.

DISCUSSION

Changes in population aspects of lutjanids, such as sex ratio, have been attributed to various factors such as differential survival by sex, distribution, habitat preference, depth, size distribution (juvenile/adult), and feeding and reproductive aspects (Lucano-Ramírez et al. 2014, Moreno-Pérez et al. 2024); a possible reason why the proportion of females and males is skewed towards one of the sexes in some months of the year

(Cruz-Romero et al. 1996, Santamaría-Miranda et al. 2003, Piñón et al. 2009, Lucano-Ramírez et al. 2023). Based on the results of this study, the above does not apply to *L. guttatus* caught on the Pacific coast of Guatemala, where the sex ratio was not statistically different from 1:1 ($P > 0.05$). Considering that this species exhibits gregarious behavior during reproductive events (Allen 1995), it is expected that the sex ratio might deviate from 1:1 during spawning. However, the number of fish sampled was relatively

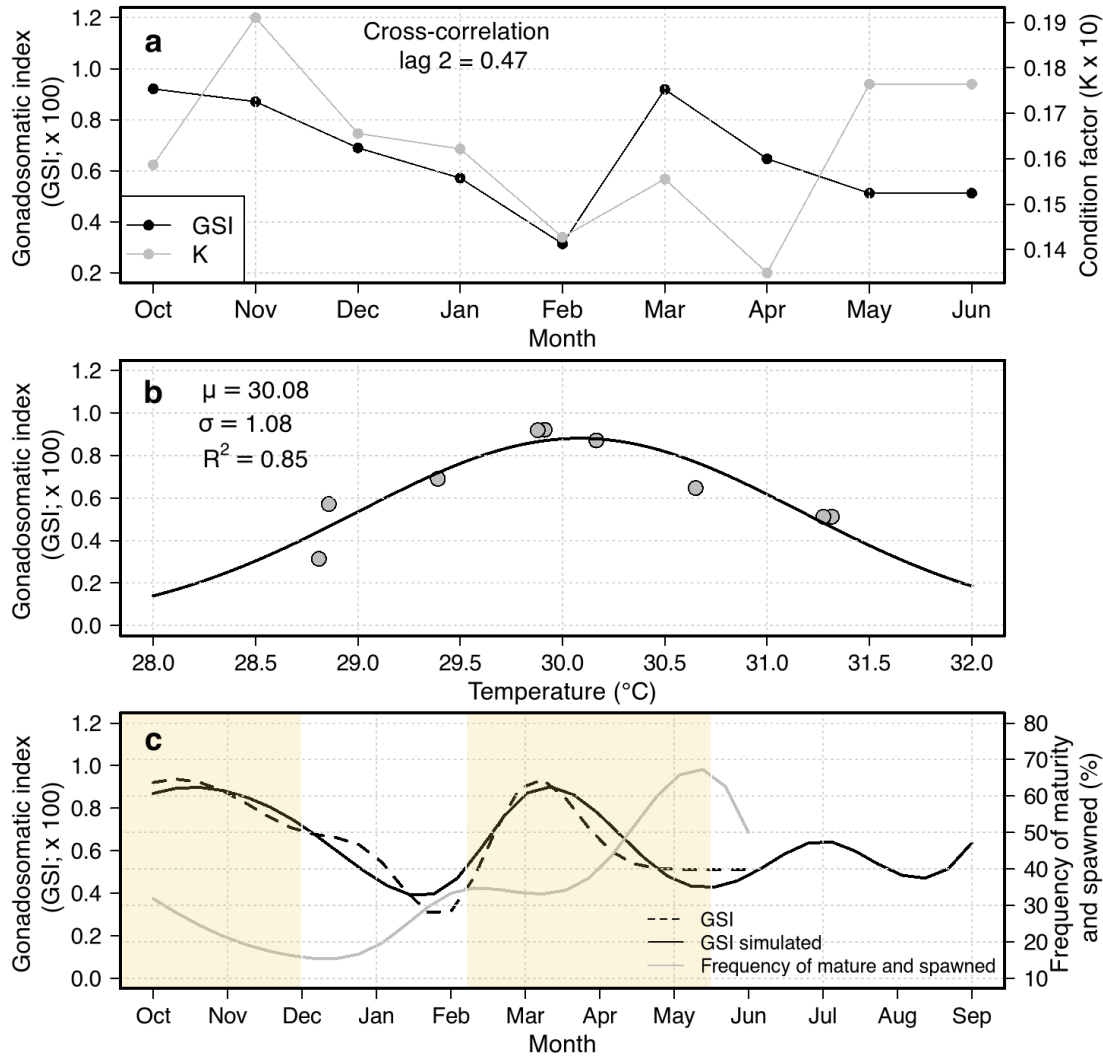


Figure 3 a) Relationship between the condition factor (K) and the gonadosomatic index (GSI) of the spotted rose snapper, *L. guttatus*, b) Gaussian relationship between mean monthly sea temperature and mean monthly GSI of the spotted rose snapper, and c) estimation of the monthly GSI of the spotted rose snapper from the average monthly temperatures of the Pacific coast of Guatemala in a typical year. The areas delineate the two reproductive periods found in this work.

low, and sex ratio differences may not have been captured. Therefore, it is important in future work to increase the sample size at the sampling sites to confirm this fact.

Oogenesis is a continuous process of ovarian maturation during which the oogonia develops into an ovule ready for ovulation (Wootton & Smith 2014). In lutjanids, it is divided into six and seven stages. The present work described six stages (nucleolar chromatic oocytes, perinuclear oocytes, cortical alveolar oocytes, vitellogenic oocytes, migratory nucleus oocytes, and hydrated oocytes). The total number of stages often depends on the species and on the criteria used by the authors to define them (González & Lugo 1997, Piñón

et al. 2009, Lucano-Ramírez et al. 2014). All these approaches consider cellular dimensions, basophilia degree, and structures such as nucleoli, vacuoles, and yolk platelets. Some studies describe a stage before the nucleolar chromoplasm, but in this work, it was not possible to observe this due to the small diameter of the cells (<4 μm) (González & Lugo 1997, Piñón et al. 2009). None of the studies have dealt in detail with the hydrated oocyte stage, possibly due to its short duration, making it difficult to observe. Hunter & Macewicz (1985) report that hydrated oocytes are expelled within 24 to 48 h and that their presence indicates spawning in females.

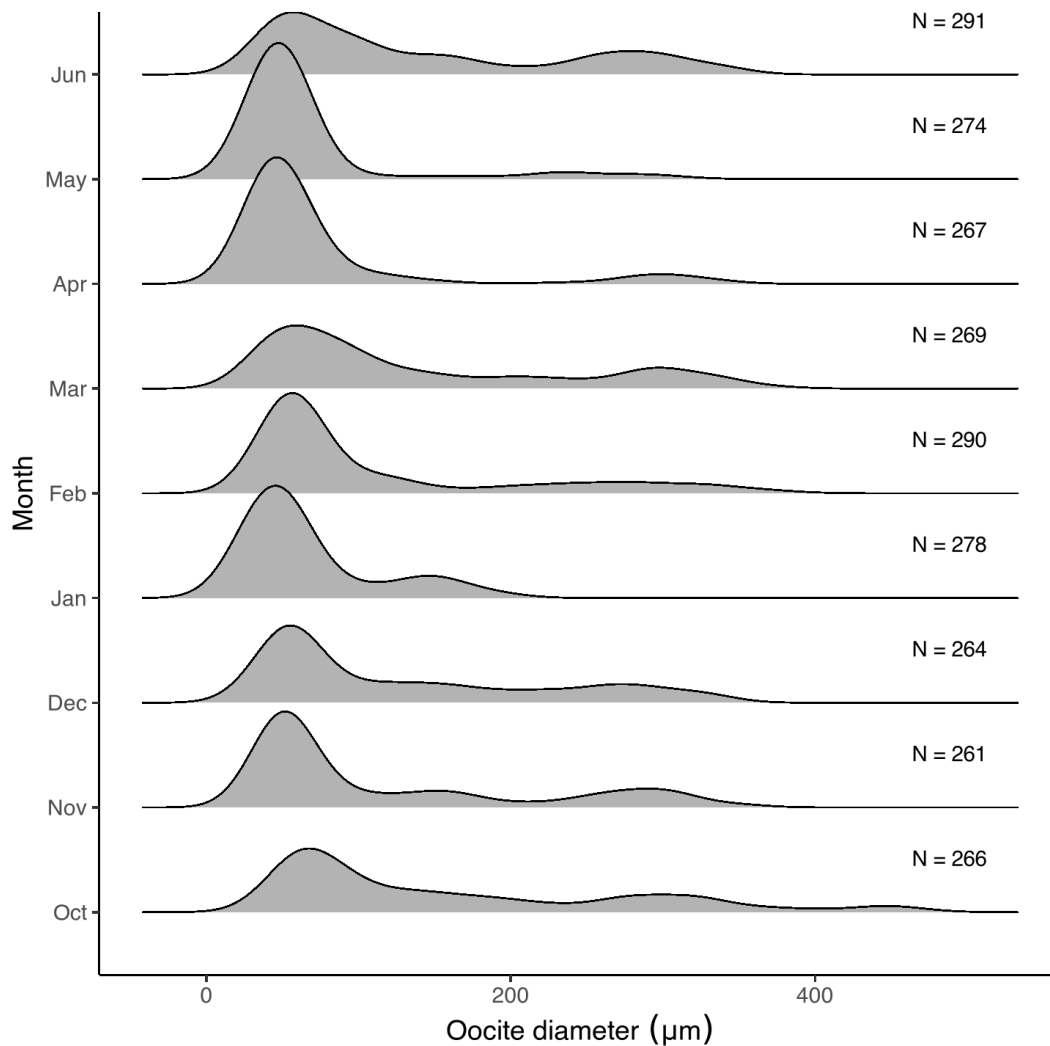


Figure 4. Distribution of the relative monthly frequencies of oocyte diameter of the spotted rose snapper, *L. guttatus*, on the Pacific coast of Guatemala. N: sample size.

Gonadal development is a continuous process, and the stages into which it is divided vary according to the criteria of the researcher and the species studied. Macroscopic analyses have been carried out, such as that on *L. fulviflamma* on the west coast of the Indian Ocean (Kaunda-Arara & Ntiba 1997) and in the Arabian Gulf (Grandcourt et al. 2006), as well as for *L. synagris* in Brazil (Freitas et al. 2014), where five phases of gonadal development were identified in both males and females. However, the importance of performing histological studies to improve the diagnosis of the different phases is recognized (Ferreri et al. 2009, Marisaldi et al. 2020, Schemmel & Brown-Peterson 2023), as was done in the present study. The histological studies carried out in the present work allowed greater precision in the diagnosis of the phases of the gonadal cycle, based mainly on the tissue and

cellular characteristics previously described for *L. guttatus* (Lucano-Ramírez et al. 2023); however, in the present work, the proportion of cells was considered to distinguish between the developmental phase and the developed phase in females. In contrast, a developed phase is described for males since the gonad continues to develop but contains many spermatozoa. The absence of a maturation phase in males and the low presence of this phase in females could be due to sampling peculiarities, possibly influenced in two ways: 1) organisms in this phase were present during the months in which sampling was not carried out, or 2) mature organisms expelled their gametes due to sources of stress such as fishing or changes in environmental conditions, which has been reported previously (Trippel 1995, 2003, Green et al. 2020).

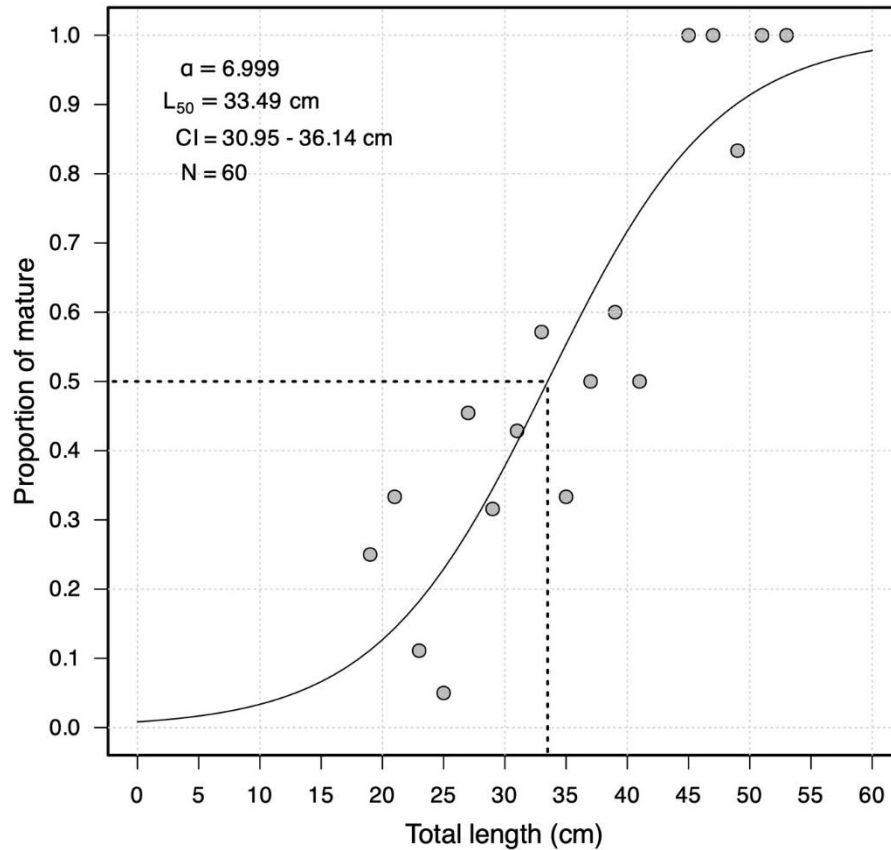


Figure 5. Early mature size of the spotted rose snapper, *L. guttatus*, on the Pacific coast of Guatemala. N: sample size, L_{50} : length at first maturity, CI: confidence interval, and α : intercept.

The gonadal development process of the spotted rose snapper on the Pacific coast of Guatemala showed similarities with other tropical fish, highlighting the presence of spawning throughout the year due to the asynchronous development of gametes (Arellano-Martínez et al. 2001, Hughes et al. 2013). Two main periods of reproductive activity were identified: one from October to December and a second from March to May. This trend was confirmed by a sustained increase in GSI to the highest point of the curve (indicating maturity), followed by a sustained decrease (as evidence of gamete expulsion) (Villalejo-Fuerte & Ceballos-Vázquez 1996) and monthly monitoring of mean oocyte diameter, confirming their effectiveness as reliable indicators of reproduction (Rodrigues et al. 2018, Salas-Singh et al. 2022, Lucano-Ramírez et al. 2023, Sultana et al. 2023), confirmed by the presence of a higher frequency of mature organisms and dose/ejaculation in these months.

It is important to note that when comparing the reproductive periods of this species in different regions of the Americas, a temporal gradient in the reproductive

period was observed. For example, the reproductive period extends from June to September in the region of Nayarit, Mexico, while this period shifts by about one month in more southern regions (Fig. 6). An analysis of Figure 6 shows that in regions with more tropical climates ($<18^{\circ}\text{N}$), this species generally has two distinct reproductive peaks, generally in spring and fall, and the Pacific coast of Guatemala was no exception (Fig. 6). This latitudinal gradient suggests the existence of several stocks with independent ecological characteristics. Therefore, based on the results of this work, it could be recommended that regionalized management would be appropriate for this resource (Li 2022).

The estimated K in the present study did not have a relationship with reproductive activity. Cushing (1975) mentions that the values of the condition of the fish can be influenced by aspects such as age, sex, gonadal cycles, and feeding rates, which could explain why other studies, such as those of Correa-Herrera & Jiménez-Segura (2013), Eraso-Ordoñez et al. (2023), and Lucano-Ramírez et al. (2023), the K can be consi-

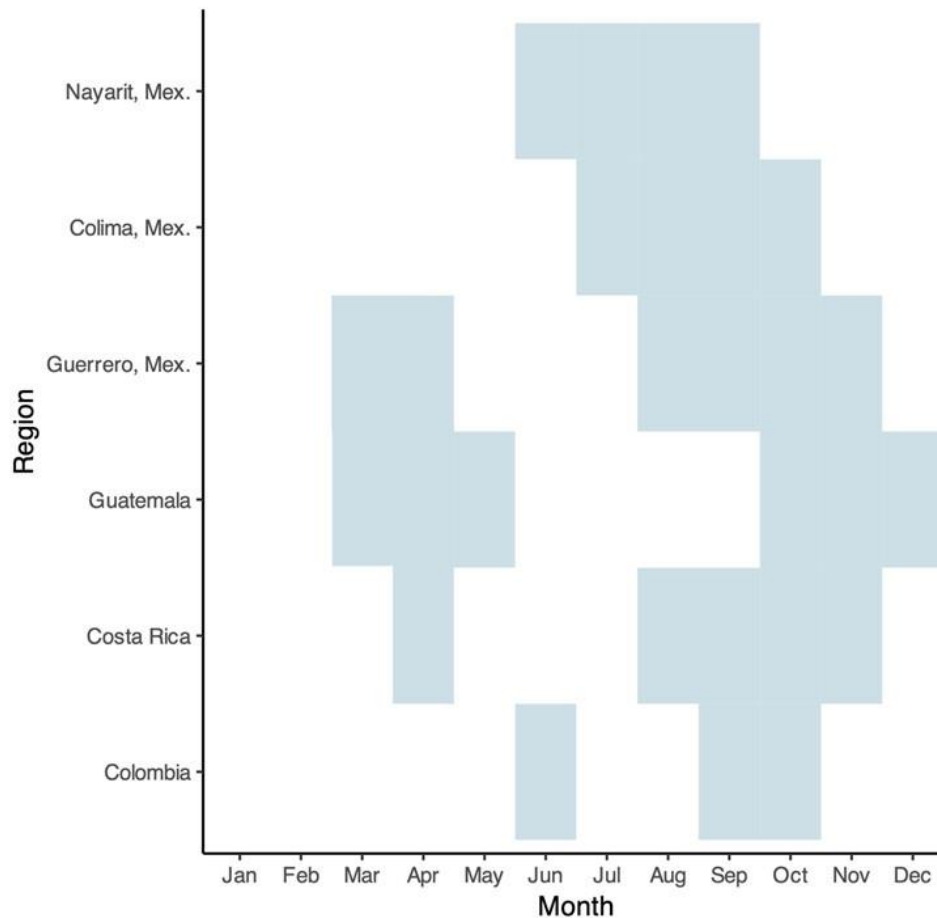


Figure 6. Comparison between the reproductive periods of different regions of the Pacific Ocean. The reproductive period of Nayarit, Mexico, was taken from Lucano-Ramírez et al. (2023); that of Colima, Mexico was taken from Cruz-Romero et al. (1998); that of Guerrero, Mexico was taken from Arellano-Martínez et al. (2001); that of Guatemala was the result of this study; that of Costa Rica was taken from Roja (1996); and that of Colombia was taken from Correa-Herrera & Jiménez-Segura (2013).

dered as an indicator of the reproductive season. In these studies, the authors attribute it to the exchange of nutrients during the process of vitellogenesis; however, in our study, we observed a process of continuous gonadal development, which suggests that the spotted rose snapper on the Pacific coast of Guatemala has enough food for gametes production without using its nutrient reserves for this purpose.

Carter & Perrine (1994) mention the influence of temperature on the reproductive cycle of *L. jocu*. This study observed that gonadal activity was low at low temperatures, with the stages of immature and development being more frequent, evidenced by the GSI. In contrast, warm temperatures (between 29 and 31°C) favored high GSI values and the presence of the stages of maturity and spawning. This last finding has been confirmed by Correa-Herrera & Jiménez-Segura

(2013) in the same species. It has also been documented for other species, such as *L. cyanopterus* (Kadison et al. 2006). In this study, we report a correlation between GSI and sea-surface temperature, suggesting that there is probably an optimal temperature range within which the reproductive periods of this species take place. Therefore, the above suggests that temperatures below 29°C and above 31°C do not favor gametogenesis processes in spotted rose snapper in the Guatemalan Pacific. Predicting reproductive behavior based on temperature changes would be possible in this context. Such predictions have been made for other marine organisms using linear relationships (Martínez-Pita & Morenos 2022). A Gaussian relationship indicates a temperature interval where reproductive periods are favored.

On the other hand, although previous studies mention that photoperiod (Rojas 1996, Aride et al. 2021, Jiang et al. 2022) and river rainfall (Arellano-Martínez et al. 2001, Soto-Rojas et al. 2009, Correa-Herrera & Jiménez-Segura 2013) are related to the reproductive period, this was not the case in the present study, maybe because increased photoperiod and riverine rainfall leads to increased productivity, resulting in greater nutrient availability (Pinckney et al. 2002, Aride et al. 2021). Thus, in areas where nutrients are scarce, organisms may use an opportunistic strategy that allows them to reproduce at the most productive times. In this study, gamete production was continuous, suggesting that nutrient availability is not a determinant of spotted rose snapper reproduction in this area.

The sizes recorded in the present study (18-53.2 cm) varied slightly between the size ranges reported by other authors for the same species. Lucano-Ramírez et al. (2023) reported sizes between 4-61 cm, Mendoza-Arzu (2018) reported 37-53.8 cm, Correa-Herrera & Jiménez-Segura (2013) reported 18-56 cm, while Rojas (1996) reported 12-60.9 cm. In this regard, Lucano-Ramírez et al. (2023) pointed out that the low variability in size is due to the similarity of the fishing gear used in the commercial fisheries from which the analyzed samples originate. In terms of first size at first maturity, the 32.8 cm estimated in the present study was lower than the 36.4 cm for females and 35.2 cm for males recorded by Mendoza-Arzu (2018) and was higher than that estimated by Correa-Herrera & Jiménez-Segura (2013) (23.5 cm), and the Lucano-Ramírez et al. (2023) estimation of 30.09 cm for females and 30.05 cm for males. There are several explanations for this discrepancy, with the main one being the number of fish sampled, which varied considerably in the four cases mentioned above. Lucano-Ramírez et al. (2023) worked with a sample of 2,889 females and 2,792 males, while Mendoza-Arzu (2018) only used 21 females and 40 males. Furthermore, Correa-Herrera & Jiménez-Segura (2013) used 93 females and 139 males; in the present study, we worked with 92 females and 87 males. On the other hand, these differences could also be attributed to spatial variation. In this sense, Saborido-Rey (2004) states that the age at first maturity varies in different populations of the same species according to the areas of their distribution range. Therefore, the variability in the length at first maturity reported above could correspond to the latitudinal gradient found (Fig. 6).

Regarding the management of the spotted rose snapper fishery in the Guatemalan Pacific, the results of this study highlight the importance of estimating a

minimum size at maturity to establish a minimum catch size and to determine reproductive seasonality to establish non-fishing periods during the identified spawning peaks, especially during March to May and October to December, which would help ensure the perpetuation of the species (Ziober et al. 2015, Erisman et al. 2017) and the fisheries. From this, it is possible to reduce the level of vulnerability of the resource to overfishing (Mohamed et al. 2021). Given that the stock status is unknown, a high level of exploitation is recognized. Based on the results of this study, a minimum catch size should be implemented to protect young individuals and to allow them to reach reproductive maturity before being captured, which would allow for maintaining a healthy population in the long term. Because sea-surface temperature is shown to be strongly correlated with spotted rose snapper reproduction, it is important to maintain constant temperature monitoring in fishing areas to identify significant changes and to temporarily adjust management measures (adaptive management) (Hernández-Padilla et al. 2022). Promoting sustainable fishing practices that minimize bycatch and the negative impacts on marine and coastal habitats is important. Establish community participation programs involving fishery management and promote collaboration between local fishers and decision-makers (co-management) to effectively implement and enforce regulations (Finkbeiner & Basurto 2015). It is a global concern, and integrative approaches to fishery management have been developed, considering fishing as a complex activity that involves interactions between resource dynamics and fishing communities. Management policies must consider this joint dynamic, balancing objectives such as conservation, income generation, and community stability. Awareness of the importance of maintaining the natural cycles of ecosystems is crucial to ensure the benefits they provide (SAGARPA 2013). These types of efforts have yielded good results, allowing the sustainability of some fisheries to be maintained (Karr et al. 2017, Cota-Nieto et al. 2018, Léopold et al. 2019). Finally, the reproductive seasonality of fishery resources is crucial for the management and conservation of species, as it allows the implementation of closures during critical periods, ensuring the sustainability of populations and biodiversity. In addition, it avoids fishing at times that would negatively affect reproductive capacity, maximizes fishing yields outside the reproductive seasons, and complies with international regulations. Knowledge of these cycles facilitates accurate monitoring and evaluation of populations, allowing for adaptive and effective management measures in time and space.

CONCLUSIONS

The present study showed that the gonadal development of the spotted rose snapper in the Guatemalan Pacific, as well as in the tropics, presents a continuous behavior of spawning throughout the year, highlighting two main periods of reproduction: one from October to December and the second from March to May. In addition, temperature was a relevant factor in reproduction, as shown by a strong correlation between GSI and gonadal development, with optimal temperature values between 29 and 31°C. It is important to continue analyzing the reproductive cycle and the environmental factors that influence the reproduction of the spotted rose snapper, as well as the impact of the management measures, including increasing the number of sampling months to gain a broader understanding of the reproductive cycle behavior. This approach aims to improve the region's potential fisheries management strategies and adapt them to new conditions. The reproductive parameters reported in this work will serve as a baseline. They will allow the establishment of management measures for science-based, relevant control of the fisheries, facilitating the fishing of this resource as a sustainable economic activity.

Credit author contribution

N. Vélez-Arellano: conceptualization, writing - original draft, visualization, validation, methodology, investigation, formal analysis; J.C. Hernández-Padilla: funding acquisition, project administration, writing - review & editing, visualization, validation, supervision, methodology, investigation, formal analysis; F. García-Domínguez: laboratory equipment, review & editing, methodology; P. Colunga-Reyes: formal analysis, methodology, investigation; N. Capetillo-Piñar: review & editing, visualization, validation; J.R. Ortiz-Aldana: review & editing, visualization, validation, investigation; N. Gijón-Yescas: review & editing, visualization, validation; I. Velázquez-Abunader: writing - review & editing, visualization, validation, supervision, methodology, formal analysis. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no potential conflict of interest in this manuscript.

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REFERENCES

- Allen, G.R. 1995. Lutjanidae. In: Fischer, W., Krupp, F., Schneider, W., Sommer, C., Carpenter, K.E. & Niem, V. (Eds.). Guía FAO para identificación de especies para los fines de la pesca. Pacífico Centro-Oriental. FAO, Rome.
- Andrade, H., Vihtakari, M. & Santos, J. 2023. Geographic variation in the life history of lane snapper *Lutjanus synagris*, with new insights from the warm edge of its distribution. *Journal of Fish Biology*, 103: 950-964. doi: 10.1111/jfb.15488
- Arellano-Martínez, M., Rojas-Herrera, A., García-Domínguez, F., Ceballos-Vázquez, B.P. & Villalejo-Fuerte, M. 2001. Ciclo reproductivo del pargo lunarejo *Lutjanus guttatus* (Steindachner, 1869) en las costas de Guerrero, México. *Revista de Biología Marina y Oceanografía*, 36: 1-8. doi: 10.4067/S0718-1957200100100001
- Aride, P.H.R., Gomes, M.F.S., Azevedo, D.G., Sangali, G.R., Silva, A.C.F., Lavander, H.D., et al. 2021. Dusky grouper *Epinephelus marginatus* growth and survival when exposed to different photoperiods. *Fishes*, 6: 1-6. doi: 10.3390/fishes6030031
- Bagenal, T.B. & Tesch, F.W. 1978. Age and growth. In: Bagenal, T. (Ed.). *Methods for assessment of fish production in freshwaters*. Blackwell Scientific Publications, New Jersey, pp. 101-136.
- Boza-Abarca, J. 2003. Manual para la reproducción y alevinaje del pargo manchado, *Lutjanus guttatus*. Universidad Nacional de Costa Rica, San José.
- Brouwer, S. & Griffiths, M. 2005. Stock separation and life history of *Argyrozona argyrozona* (Pisces:

- Sparidae) on the South African east coast. *African Journal of Marine Science*, 27: 585-595. doi: 10.2989/18142320509504119
- Brulé, T., Renán, X. & Colás-Marrufo, T. 2022. Potential impact of climate change on fish reproductive phenology: A case study in gonochoric and hermaphrodite commercially important species from the southern Gulf of Mexico. *Fishes*, 7: 156. doi: 10.3390/fishes7040156
- Carter, J. & Perrine, D. 1994. A spawning aggregation of dog snapper, *Lutjanus jocu* (Pisces: Lutjanidae) in Belize, Central America. *Bulletin of Marine Sciences*, 55: 228-234.
- Correa-Herrera, T. & Jiménez-Segura, L.F. 2013. Reproductive biology of *Lutjanus guttatus* (Perciformes: Lutjanidae) in Utría National Park, Colombian Pacific. *Revista de Biología Tropical*, 61: 829-840.
- Cota-Nieto, J.J., Erisman, B., Aburto-Oropeza, O., Moreno-Báez, M., Hinojosa-Arango, G. & Johnson, A.F. 2018. Participatory management in a small-scale coastal fishery-Punta Abrejos, Pacific coast of Baja California Sur, Mexico. *Regional Studies in Marine Science*, 18: 68-79. doi: 10.1016/j.rsma.2017.12.014
- Cruz-Romero, M., Chávez, E.A., Espino, E. & García, A. 1996. Assessment of a snapper complex (*Lutjanus* spp.) of the eastern tropical Pacific. In: Arreguín-Sánchez, F., Munro, J.L., Balgos, M.C. & Pauly, D. (Eds.). *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM, Municipality of Los Baños, pp. 324-330.
- Cushing, D.H. 1975. *Marine ecology and fisheries*. Cambridge University Press, Cambridge.
- Dirección de Normatividad de la Pesca y Acuicultura/Ministerio de Agricultura, Ganadería y Alimentación (DIPESCA/MAGA). 2018. Caracterización de la pesca artesanal en el Pacífico de Guatemala. Proyecto "Conservación y Uso Sostenible de la Biodiversidad en Áreas Protegidas Marino Costeras (APM's)". DIPESCA/MAGA, Ciudad de Guatemala.
- Eraso-Ordoñez, J.F., Yee-Duarte, J.A., Roldán-Wong, N.T., García-Ulloa, M., Góngora-Gómez, A.M. & Arellano-Martínez, M. 2023. Histopathological alterations in the gonads of wild white clams *Dosinia ponderosa* inhabiting a former copper mine locality in the Gulf of California. *Journal of Aquatic Animal Health*, 35: 101-116. doi: 10.1002/aah.10184
- Erisman, B., Heyman, W., Kobara, S., Ezer, T., Pittman, S., Aburto-Oropeza, O., et al. 2017. Fish spawning aggregations: where well-placed management actions can yield big benefits for fisheries and conservation. *Fish and Fisheries*, 18: 128-144. doi: 10.1111/faf.12132
- Fernandes, J.F.F., Freitas, J., de Araújo, S.A., de Santana, T.C., Lobato, R.S. & Figueiredo, M.B. 2022. Reproductive biology of the lane snapper, *Lutjanus synagris* (Linnaeus, 1758) (Perciformes, Lutjanidae), in the Maranhão continental shelf, northeast of Brazil. *Environmental Biology of Fishes*, 105: 1033-1050. doi: 10.1007/s10641-022-01310-z
- Ferreri, R., Basilone, G., D'Elia, M., Traina, A., Saborido-Rey, F. & Mazzola, S. 2009. Validation of macroscopic maturity stages according to microscopic histological examination of European anchovy. *Marine Ecology*, 30: 181-187. doi: 10.1111/j.1439-0485.2009.00312.x
- Finkbeiner, E.M. & Basurto, X. 2015. Re-defining co-management to facilitate small-scale fisheries reform: an illustration from northwest Mexico. *Marine Policy*, 51: 433-441. doi: 10.1016/j.marpol.2014.10.010
- González, L.W. & Lugo, T. 1997. Ovogenesis de *Lutjanus purpureus* Poey, 1867 (Pisces: Lutjanidae) de la región oriental de Venezuela. *Boletín de Investigaciones Marinas y Costeras - INVEMAR*, 26: 53-60.
- Grandcourt, E.M., Abdessalaam, T.Z. & Francis, F. 2006. Age, growth, mortality and reproduction of the blackspot snapper, *Lutjanus fulvivlamma* (Forsskål, 1775), in the southern Arabian Gulf. *Fisheries Research*, 78: 203-210. doi: 10.1016/j.fishres.2005.11.021
- Green, L., Havenhand, J.N. & Kvarnemo, C. 2020. Evidence of rapid adaptive trait change to local salinity in the sperm of an invasive fish. *Evolutionary Applications*, 13: 533-544. doi: 10.1111/eva.12859
- Hernández-Padilla, J.C., Capetillo-Piñar, N., Aranceta-Garza, F., Yee-Duarte, J.A., Vélez-Arellano, N. & Velázquez-Abunader, I. 2020. Length-weight relationships of 12 marine fish species from the Pacific coast of Guatemala associated with small-scale fisheries. *Journal of Applied Ichthyology*, 36: 863-865. doi: 10.1111/jai.14093
- Hernández-Padilla, J.C., Arreguín-Sánchez, F., Zetina-Rejón, M.J., Seijo, J.C., Cisneros-Montemayor, A., Capetillo-Piñar, N., et al. 2022. Is it possible to use fisheries management reference points based on changes in ecosystem structure and function? The effect of climate change. *Ciencia Pesquera*, 30: 55-77.
- Hijmans, R. 2023. Raster: Geographic data analysis and modeling (3.6-23). [https://CRAN.R-project.org/package=raster]. Reviewed: March 13, 2024.
- Hughes, R.N., Hughes, D. & Smith, I.P. 2013. Biogeography of transient reef-fish spawning aggregations in the Caribbean: a synthesis for future research and management. *Oceanography and Marine Biology: An Annual Review*, 51: 281-326.

- Humason, L.G. 1979. Animal tissue techniques. W.H. Freeman, San Francisco.
- Hunter, J.R. & Macewicz, B.J. 1985. Measurement of spawning frequency in multiple spawning fishes. NOAA Technical Report NMFS, 36: 79-94.
- Jiang, M., Chen, H., Zhou, S., Han, Q., Peng, R. & Jiang, X. 2022. Changes in embryonic development, juvenile growth and physiological adaptation of the cuttlefish *Sepia pharaonis* in response to photoperiod manipulation. *Journal of Oceanology and Limnology*, 40: 2012-2027. doi: 10.1007/s00343-021-1243-2
- Kadison, E., Nemeth, R.S., Herzlieb, S. & Blondeau, J. 2006. Temporal and spatial dynamics of *Lutjanus cyanopterus* (Pisces: Lutjanidae) and *L. jocu* spawning aggregations in the United States Virgin Islands. *Revista de Biología Tropical*, 54: 69-78.
- Karr, K.A., Fujita, R., Carcamo, R., Epstein, L., Foley, J.R., Fraire-Cervantes, J.A., et al. 2017. Integrating science-based co-management, partnerships, participatory processes and stewardship incentives to improve the performance of small-scale fisheries. *Frontiers in Marine Science*, 4: 1-9. doi: 10.3389/fmars.2017.00345
- Kaunda-Arara, B. & Ntiba, M.J. 1997. The reproductive biology of *Lutjanus fulvivflamma* (Forsskål, 1775) (Pisces: Lutjanidae) in Kenyan inshore marine waters. *Hydrobiologia*, 353: 153-160. doi: 10.1023/A:1003011013136
- Kjesbu, O.S. 2016. Applied fisheries reproductive biology: Contribution of individual reproductive potential to recruitment and fisheries management. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A. & Moksness, E. (Eds.). *Fish reproductive biology: Implications for assessment and management*. Wiley, New York, pp. 321-366.
- Léopold, M., Thébaud, O. & Charles, A. 2019. The dynamics of institutional innovation: crafting co-management in small-scale fisheries through action research. *Journal of Environmental Management*, 237: 187-199. doi: 10.1016/j.jenvman.2019.01.112
- Li, S. 2022. Incorporation of fisheries policy into regional blocs?-Lessons from the EU's Common Fisheries Policy. *Fishes*, 7: 1-18. doi: 10.3390/fishes7030102
- Lowerre-Barbieri, S., Crabtree, L., Switzer, T., Walters-Burnsed, S. & Guenther, C. 2015. Assessing reproductive resilience: an example with South Atlantic red snapper *Lutjanus campechanus*. *Marine Ecology Progress Series*, 526: 125-141. doi: 10.3354/meps11212
- Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I.A., Muhling, B., Erisman, B., et al. 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. *Fish and Fisheries*, 18: 285-312. doi: 10.1111/faf.12180
- Lucano-Ramírez, G., Ruiz-Ramírez, S., González-Sansón, G. & Ceballos-Vázquez, B.P. 2014. Reproductive biology of the yellow snapper, *Lutjanus argentiventris* (Pisces, Lutjanidae), from the Mexican central Pacific. *Ciencias Marinas*, 40: 33-44. doi: 10.7773/cm.v40i1.2325
- Lucano-Ramírez, G., Ruiz-Ramírez, S., Rojo-Vázquez, J.A., Lara-Mendoza, R.E., Aguilar-Betancourt, C.M. & González-Sansón, G. 2023. Reproduction of *Lutjanus guttatus* (Perciformes: Lutjanidae) captured in the Mexican Central Pacific. *Latin American Journal of Aquatic Research*, 51: 503-520. doi: 10.3856/vol51-issue4-fulltext-3008
- Marisaldi, L., Basili, D., Candelma, M., Sesani, V., Pignalosa, P., Gioacchini, G., et al. 2020. Maturity assignment based on histology-validated macroscopic criteria: Tackling the stock decline of the Mediterranean swordfish (*Xiphias gladius*). *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30: 303-314. doi: 10.1002/aqc.3248
- Marshall, C.T. 2009. Implementing information on stock reproductive potential in fisheries management: The motivation, challenges and opportunities. In: Jakobsen, T., Fogarty, M.J., Megrey, B.A. & Moksness, E.S. (Eds.). *Fish reproductive biology*. Wiley-Blackwell, Oxford, pp. 395-420.
- Martínez-Pita, I. & Moreno, O. 2022. A method to predict the reproductive cycle of the striped venus clam *Chamelea gallina* based on the influence of environmental factors: Application in its fishery management. *Fisheries Research*, 245: 106-133. doi: 10.1016/j.fishres.2021.106133
- Mendoza-Arzu, M.J. 2018. Estimación de la talla de primera madurez sexual del pargo *Lutjanus guttatus* (Steindachner, 1869) y del ronco *Pomadasys panamensis* (Steindachner, 1876) validado por cortes histológicos. Tesis de Licenciatura, Universidad de San Carlos de Guatemala, Ciudad de Guatemala.
- Mohamed, K.S., Sathianandan, T.V., Vivekanandan, E., Kuriakose, S., Ganga, U., Pillai, S.L., et al. 2021. Application of biological and fisheries attributes to assess the vulnerability and resilience of tropical marine fish species. *Plos One*, 16: 255879. doi: 10.1371/journal.pone.0255879
- Moreno-Pérez, I.J., López-Martínez, J., Padilla-Serrato, J.G., Rodríguez-Romero, J., Barjau-González, E. & Arreola-Lizárraga, J.A. 2024. Fish community, seasonal movement and habitat use in a subtropical coastal lagoon. *Latin American Journal of Aquatic Research*, 52: 1-14. doi: 10.3856/vol52-issue1-fulltext-3108

- Oliveira-Freitas, M., Rodrigues-Alves-Rocha, G., Da Cunha-Chaves, P.D.T. & Da Moura, R.L. 2014. Reproductive biology of the lane snapper, *Lutjanus synagris*, and recommendations for its management on the Abrolhos Shelf, Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 94: 1711-1720. doi: 10.1017/S0025315414001088
- Pinckney, J.L., Paerl, H.W. & Harrington, M.B. 2002. Responses of the phytoplankton community growth rate to nutrient pulses in variable estuarine environment. *Journal of Phycology*, 35: 1455-1463. doi: 10.1046/j.1529-8817.1999.3561455.x
- Piñón, A., Amezcua, F. & Duncan, N. 2009. Reproductive cycle of female yellow snapper *Lutjanus argentiventris* (Pisces, Actinopterygii, Lutjanidae) in the SW Gulf of California: gonadic stages, spawning seasonality and length at sexual maturity. *Journal of Applied Ichthyology*, 25: 18-25. doi: 10.1111/j.1439-0426.2008.01178.x
- R Core Team. 2024. R: A language and environment for statistical computing (4.2.2). R Foundation for Statistical Computing, Vienna. [https://www.R-project.org/]. Reviewed: February 28, 2024.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. In: Stevenson, J.C. (Ed.). *Fisheries Research Board of Canada Bulletin*, 191: 14 pp.
- Rodrigues, K.A., Leonarduzzi, E., Macchi, G.J. & Militelli, M.I. 2018. Maternal condition, fecundity and oocyte quality of Argentine hake (*Merluccius hubbsi*) from the northern stock. *Fisheries Research*, 197: 105-112. doi: 10.1016/j.fishres.2017.09.005
- Rojas, J.R. 1996. Fecundidad y épocas de reproducción del "pargo mancha" *Lutjanus guttatus* (Pisces: Lutjanidae) en el Golfo de Nicoya, Costa Rica. *Revista de Biología Tropical*, 44: 477-487.
- Russell, D.J. & McDougall, A.J. 2008. Reproductive biology of mangrove jack (*Lutjanus argentimaculatus*) in northeastern Queensland, Australia. *New Zealand Journal of Marine and Freshwater Research*, 42: 219-232. doi: 10.1080/00288330809509950
- Saborido-Rey, F. 2004. Ecología de la reproducción y potencial reproductivo en las poblaciones de peces marinos. Instituto de Investigaciones Marinas (CSIC) - Universidad de Vigo, Vigo.
- Salas-Singh, C., Morales-Bojórquez, E. & Aguirre-Villaseñor, H. 2022. Reproductive biology of the bullseye puffer *Sphoeroides annulatus*: Gonadosomatic index and its suitability for estimating length at maturity. *Journal of Fish Biology*, 101: 1119-1133. doi: 10.1111/jfb.15174
- Santamaría-Miranda, A., Elorduy-Garay, J.F., Villalejo-Fuerte, M. & Rojas-Herrera, A.A. 2003. Desarrollo gonadal y ciclo reproductivo de *Lutjanus peru* (Pisces: Lutjanidae) en Guerrero, México. *Revista de Biología Tropical*, 51: 489-502.
- Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA). 2013. Huachinango del Pacífico centro-sur costa de Nayarit a Chiapas. In: Beléndez-Moreno, L.F.J., Espino-Barr, E., Galindo-Cortes, G., Gaspar-Dillanes, M.T., Huidobro-Campos, L. & Morales-Bojórquez, E. (Eds.). *Sustentabilidad y pesca responsable en México. Evaluación y manejo*. INAPESCA, Ciudad de México, pp. 140-173.
- Schemmel, E. & Brown-Peterson, N.J. 2023. Handling effects on histological identification of female reproductive status: Examples from tropical deepwater snappers. *Fishes*, 8: 1-20. doi: 10.3390/fishes8080406
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. W.H. Freeman and Company, New York.
- Somarakis, S., Tsoukali, S., Giannoulaki, M., Schismenou, E. & Nikolioudakis, N. 2019. Spawning stock, egg production and larval survival in relation to small pelagic fish recruitment. *Marine Ecology Progress Series*, 617: 113-136. doi: 10.3354/meps12642
- Soto-Rojas, R.L., Mejía-Arana, F., Palacios, J.A. & Hiramatsu, K. 2009. Reproducción y crecimiento del pargo mancha *Lutjanus guttatus* (Pisces: Lutjanidae) en el Golfo de Nicoya, Costa Rica. *Revista de Biología Tropical*, 57: 125-131.
- Sultana, T., Mazumder, S.K., Kubra, J., Nishad, N., Khalil, S.M.I., Das, S.K., et al. 2023. A multidisciplinary method to assess the reproductive biology of *Mystus bleekeri*. *Aquaculture and Fisheries*, 8: 280-287. doi: 10.1016/j.aaf.2021.12.017
- Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. *BioScience*, 45: 759-771. doi: 10.2307/1312628
- Trippel, E.A. 2003. Estimation of male reproductive success of marine fishes. *Journal of Northwest Atlantic Fishery Science*, 33: 81-113.
- Villalejo-Fuerte, M. & Ceballos-Vázquez, B.P. 1996. Variación de los índices de condición general, gonádico y de rendimiento muscular en *Argopecten circularis* (Bivalvia: Pectinidae). *Revista de Biología Tropical*, 44: 591-594.
- White, D.B. & Palmer, S.M. 2004. Age, growth, and reproduction of the red snapper, *Lutjanus campechanus*, from the Atlantic waters of the southeastern U.S. *Bulletin of Marine Sciences*, 75: 335-360.
- Wilke, C. 2024. ggridges: Ridgeline Plots in 'ggplot2'. R package version 0.5.6. [https://CRAN.R-project.org/package=ggridges>]. Reviewed: February 28, 2024.

Wootton, R.J. & Smith, C. 2014. Reproductive biology of teleost fishes. John Wiley & Sons, New Jersey.

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Ziober, S.R., Reynalte-Tataje, D.A. & Zaniboni-Filho, E. 2015. The importance of a conservation unit in a subtropical basin for fish spawning and growth. *Environmental Biology of Fishes*, 98: 725-737. doi: 10.1007/s10641-014-0307-y