Latin American Journal of Aquatic Research, 53(4): xxx-xxx, 2025
DOI: 10.3856/vol53-issue4-fulltext-3350

Research Article

Reproductive cycle of the gastropod *Opeatostoma pseudodon* (Burrow, 1815) from the artisanal fishery at Puerto Ángel, Oaxaca, Mexico

Verónica Mitsui Saito-Quezada[1,2], Esther Uría-Galicia[3], José Luis Gómez-Márquez[4]
Ana Bertha Villaseñor-Martínez[5], María de Lourdes Jiménez-Badillo[6]
Laura Elena Sanvicente-Añorve[7] & Isaías Hazarmabeth Salgado-Ugarte[2]
[1]Posgrado en Ciencias Biológicas, Unidad de Posgrado, Circuito de Posgrado, Coyoacán, México
[2]Laboratorio de Biometría y Biología Pesquera, FES Zaragoza
UNAM, Iztapalapa, Ciudad de México, México
[3]Laboratorio de Histología, Departamento de Morfología, ENCB, IPN
Santo Tomás, Ciudad de México, México
[4]Laboratorio de Limnología, FES Zaragoza, Universidad Nacional Autónoma de México, Iztapalapa, México
[5]Departamento de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México
Ciudad de México, México
[6]Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Veracruz, México
[7]Laboratorio de Ecología de Sistemas Pelágicos, Instituto de Ciencias del Mar y Limnología
Universidad Nacional Autónoma de México, Coyoacán, México
Corresponding author: Isaías Hazarmabeth Salgado-Ugarte (isalgado@unam.mx)

ABSTRACT. We studied the reproductive cycle of 1,604 ind of *Opeatostoma pseudodon* from the artisanal fishery in Puerto Ángel, Oaxaca, Mexico, using gonadal histology over two years. The sex ratio was slightly skewed towards males, who were more abundant from June to August; thereafter, females outnumbered them. Histological gonadal stages included initial oogenesis, vitellogenic maturity, maturity, spawning, and rest; spermatogenesis, maturity, spawning, and rest. Cross-correlation analysis revealed significant delays between peak spawning and resting stage frequencies, indicating that females require longer to reach maturity than males, but rest for one month less after spawning. High chlorophyll-*a* concentrations resulting from winter upwelling were significantly and synchronously cross-correlated with high numbers of mature individuals. Furthermore, cross-correlation analysis revealed that the high frequencies of mature individuals occurred six months after the highest monthly temperatures (May to August), during the coolest months (October to March). The opposite was true for the frequency of resting organisms (high during warm months, low during cool months). Due to the narrow temperature range of the studied sites, food availability seems to be the main trigger for the onset of reproduction. We hope this study will provide information on reproduction (stages and timing) useful for proposing management strategies (winter ban) and aquaculture potential.

Keywords: *Opeatostoma pseudodon*; sexual: l proportion; maturity stages; histological analysis; nonlinear resistant smoothing; cross correlation

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Associate Editor: César Lodeiros

INTRODUCTION

Marine mollusks are among the most important invertebrate fisheries in the world (Leiva & Castilla 2002). It is reported that the mollusks represent 7.8% of the world's total marine capture production, a figure slightly higher than that of crustaceans (7.1%) (FAO 2024). In addition, mollusks play a crucial social role as part of artisanal fisheries (Leiva & Castilla 2002). In Mexico, the catch of gastropods rose from the 28th position in importance, with 14,887 t in 2021, to the 12th position (21,359 t) in 2023 (SAGARPA 2021, 2023). The mollusk gastropod *Opeatostoma pseudodon* (Burrow, 1815) is caught by artisanal fisheries for local and tourist consumption in the states of Oaxaca and Guerrero, Mexico (Villegas-Maldonado et al. 2007, Flores-Garza et al. 2012, Torreblanca-Ramírez et al. 2014).

O. pseudodon, commonly known as "thorn latirus" or locally named "caracol colmillo de perro" (in Spanish), is a carnivorous gastropod with a corneous operculum (Harasewych & Moretzsohn 2010); its shell is white with slightly raised, dark brown spiral chords under a yellowish- brown periostracum with a short or long toothlike spine (hence its name) at the base of the outer lip. It is distributed from Cabo San Lucas, Baja California Sur, Gulf of California (Mexico), to Peru (Keen 1971, Dance 2002, Harasewych & Moretzsohn 2010).

Studies on the vertical distribution, abundance, density, and habitat of this species have been conducted throughout its distribution range. In Costa Rica, Bakus (1968) and Salcedo-Martínez et al. (1988), and in the Mexican Pacific, Esqueda et al. (2000), Willis & Cortés (2001), Valdés-González et al. (2004), González-Villareal (2005), Ríos-Jara et al. (2006), López-Uriarte et al. (2007), Torreblanca-Ramírez et al. (2012), and Flores-Rodríguez et al. (2014) have conducted research in this area. Other authors report its occurrence in Ecuador (Shasky 1984), Costa Rica (Roe 1988, Willis & Cortés 2011), and the Mexican Pacific (Biasca 1983, De León-Herrera 2000, Bautista-Moreno & Lechuga-Medina 2007, Caicedo-Rivas et al. 2007, Pérez-Peña et al. 2007, Ramírez-González & Barrientos-Luján 2007). Reports on the feeding habits of *O. pseudodon* include contributions from Paine (1966), Spight (1979), and Vermeij (2001). Regarding certain anatomical aspects, studies have been conducted in Mexico (Landa-Jaime 2007) and Panama (Price 2003, Kosyan et al. 2009). Flores-Rodríguez et al. (2014) have also documented the presence of the species at Puerto Ángel, Oaxaca, México. Additionally, Guzmán-Urieta (2015) conducted a study on the age and growth of the species.

The study of the reproductive cycle of marine organisms is a fundamental topic in fisheries science. It provides insight into the optimal timing for harvesting specific species, intending to prevent population decline. Information on the reproductive biology of *O. pseudodon* is currently limited. In the absence of fishery-biological knowledge, it is crucial to analyze the reproductive characteristics of the species to implement targeted catch measures that achieve sustainable exploitation (Elhasni et al. 2013). The objective of this study is then to investigate the reproductive cycle of *O. pseudodon*, analysing the histological gonad stages of specimens obtained from the artisanal fishery at Puerto Ángel, Oaxaca, Mexico, and their relationship with sea surface temperature and chlorophyll-*a* (Chl-*a*) concentration along two annual periods (2014-2015). This report constitutes an addition to a similar previous paper on the reproductive cycle of another gastropod species (*Hexaplex princeps*) from the same locality (Saito-Quezada et al. 2018).

MATERIALS AND METHODS

The specimens were obtained from the artisanal fishery with (as much as possible) monthly periodicity during two annual periods from January 2014 to December 2015. The organisms were caught with the help of two local free divers at depths ranging from 5 to 15 m in rocky coastal areas in the vicinity of Puerto Ángel, Oaxaca, México (Table 1, Fig. 1). As reported by García (2004) and the Servicio Meteorológico Nacional (CONAGUA 2024) the local meteorological station data for Puerto Ángel (15°39'N, 96°29'W), indicate a tropical climate with the highest mean monthly temperature occurring in May (28.7°C) and minimum in January (26.4°C); the mean annual temperature is 27.5°C with an annual precipitation of 905.5 mm (from 0.8 mm in April to 250.6 mm in September). It has a dry season (November-April) and a wet season (May-October), with a particularly hot period (July-August). The collecting sites were selected each day according to the atmospheric and sea conditions, as well as the diver's knowledge of the species' availability in the zone. We aimed to collect a representative number of specimens from the region to gather biological information for histological analysis of gametes.

The captured organisms were placed in thermic recipients with a frigorifidal mixture (ice-NaCl) for their transportation to the laboratory. A subsample of individuals with shell lengths larger than approximately 3 cm was selected for the extraction of soft parts, which was achieved by breaking the shell and fixing it in a

Table 1. Specimen sampling and environmental variables (surface sea temperature and chlorophyll-a) measure site geopositions.

Site	Latitude (N)	Longitude (W)
Punta Cometa (PC)	15°39'35.4"	96°33'16.5"
San Agustinillo (SA)	15°39'48.6"	96°33'01.0"
Playa Panteón (PP)	15°39'56.1"	96°29'27.1"
Aragón (Ar)	15°39'38.2"	96°31'46.8"
Estacahuite (Es)	15°40'04.7"	96°28'54.5"
Bajos de Aceite (BA)	15°40'10.6"	96°28'29.6"
La Mina (LM)	15°40'26.7"	96°28'35.7"
La Boquilla (LB)	15°40'48.3"	96°27'58.4"
Secretario (Sr)	15°41'02.3"	96°27'00.5"
Tijera (Tj)	15°41'20.2"	96°26'26.3"
Dominguillo (Dm)	15°41'35.0"	96°26'02.2"
Playita, Tembo (PT)	15°41'36.1"	96°25'54.3"
Temperature and chlorophyll-*a*, (TC)	15°39'01.0"	96°28'45.0"

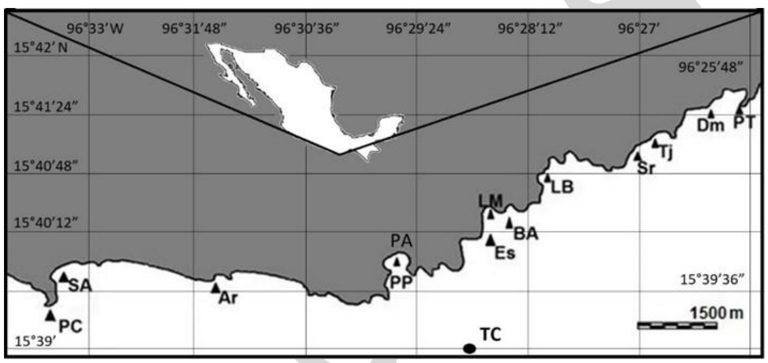

Figure 1. Geographical location of the study area, Puerto Ángel (PA), Oaxaca, Mexico. Temperature-chlorophyll concentration (TC) and sampling sites are indicated. PC: Punta Cometa, SA: San Agustinillo, Ar: Aragón, PP: Playa Panteón, Es: Estacahuite, LM: La Mina, BA: Bajos de Aceite, LB: La Boquilla, Sr: Secretario, Tj: Tijera, Dm: Dominguillo, PT: Playita Tembo.

10% formaldehyde solution with seawater (Ortíz-Ordóñez et al. 2009, Vasconcelos et al. 2012). Once the specimens had thawed, their shell length (SL) was measured to the nearest 0.01 mm using a digital caliper, and their total weight (TW) was recorded to the nearest 0.01 g using a top-loading digital balance. The soft parts were extracted either by direct manipulation or by breaking the shell. Once the specimens were extracted from the shell, the operculum, visceral coil (comprising the gonad and digestive gland), foot, mantle, and muscle (callus) were separated and weighed using a semi-analytical balance with a precision of 0.001 g. The individuals were sexed based on the presence or absence of the penis. The *in situ* subsampled fixed individuals' soft parts, which were allowed to rest for 48 h, were then washed and preserved in 70% alcohol. The preserved samples were dehydrated using the standard alcohol series (70-100%) and then cleared in xylol. Subsequently, they were bisected along a transverse plane to the visceral coil (comprising the digestive gland and gonad) to facilitate inclusion with Paraplast. Paraffin sections of 5 µm thickness were prepared and stained with the hematoxylin-eosin technique. The stained sections were mounted on glass slides following the methodology described by Uría-Galicia & Mora-Vázquez (1996). The sections were then fixed with Entellan and covered with glass slides. Finally, the preparations were observed and photographed using an optical microscope (Olympus EX41) equipped with a camera attachment. As no previously published gonad maturation stage classifications exist for this species, we considered several reproductive features to establish a classification system for it. These included the gametes' developmental stage, presence, abundance, and the characteristics of the associated tissues (Pérez-Sarabia et al. 2012), as well as a comparison with classifications established for other mollusk species (Carreón-Palau et al. 2003, Baqueiro-Cárdenas et al. 2005, Vasconcelos et al. 2012).

The sea surface temperature and Chl-*a* concentration at Puerto Ángel were obtained from the GES DISC-NASA database (2016a,b). The monthly mean values were obtained from a site near Puerto Angel Bay (Fig. 1, Table 1).

To clarify the temporal patterns throughout the study period, we employed the nonlinear resistant smoother "4253EH,twice" which is a combination of several smoothing techniques, which includes the smooth result of even span running median smoothers (4,2), the resistance of odd running medians (5,3) with end point adjustment (e), the "Hanning" weighted mean smoother (h) and the "re-roughing" (twice) step (Velleman & Hoaglin 1981, Goodall 1990, Salgado-Ugarte & Curts-García 1992, 1993, Salgado-Ugarte 2017, Salgado-Ugarte & Saito-Quezada 2020). As the smoother requires continuous data series, a simple averaging of nearest points procedure was employed to fill the occasional gaps. To assess the statistical significance of the relationships between the morpho-physiological indices, frequency maturity stages, temperature, and Chl-*a* concentration mean values, time series cross-correlation analysis was applied (Davis 2002, Becketti 2013).

RESULTS

Sex ratio

A total of 768 ind (409 males and 359 females) were captured. During the first and last months of 2014, a male predominance was observed, with a ratio of approximately 3:2 to 5:2. For the remaining months, there was no significant departure from the 1:1 sex ratio. The total sex ratio of 1.14:1.00 indicated a slight male dominance, which was statistically significant only at the 0.10 level (Table 2).

Reproductive cycle

The identification and characterization of the phases of gonadal development were completed in 300 ind. The different stages of gonadal development were classified according to the presence and abundance of gametes. The female reproductive cycle was observed to comprise five stages (Table 3, Fig. 2), namely: initial oogenesis (S1), vitellogenic maturity (S2), maturity (S3), spawning (S4), and rest (S5). In contrast, the male reproductive cycle was observed to comprise four stages (Table 4, Fig. 3), namely initial spermatogenesis (S1), maturity (S2), spawning (S3), and rest (S4).

During 2014, according to the stage frequency, females of *O. pseudodon* reproduced throughout the year, except in July. The months with the highest spawning percentages were January (60%), May (70%), November, and December (80%). The resting phase occurred from January to October, with the months showing the highest frequencies being April (70%) and July (100%). In 2015, the reproductive stages occurred almost throughout the year, except in August, and the highest reproductive frequencies occurred in January, February, and November (each at 70%). This year, the resting period was broader from January to November, but in contrast to 2014, lower frequencies were observed. Nevertheless, the months with higher frequencies were April (50%) and July (70%) (Fig. 4).

For males, in 2014, it was observed that they maintained a reproductive condition for almost the entire year, except for July. The months with the highest spawning frequency were January (60%), May (70%), November (80%), and December (70%). In 2015, the reproductive stages occurred throughout the year, except in July. The months with a higher spawning frequency (stage 3) were January (60%) and May, October, and November, each with a frequency of 80%. In 2014, the resting phase occurred from January to October, with the highest frequencies in April (40%) and July (100%). In 2015, the resting stage occurred from January to August, with April (30%) and July (70%) having the highest frequencies (Fig. 5).

Chlorophyll-*a* (Chl-*a*) concentration and gonadal cycle

Females

In 2014, high Chl-*a* concentrations were observed in January, February, March, and December (3.01, 4.00, 2.05, and 2.27 mg m^{-3}, respectively). Correspondingly, the higher frequency peaks of spawning (S4) occurred in January (60%) and December (80%). On the other hand, the lowest chlorophyll concentrations were observed in June (0.15 mg m^{-3}) and July (1.11 mg m^{-3}), with the highest resting (S5) frequency (100%) occurring in July (Fig. 4).

In 2015, high concentrations were observed in January, February, and April (1.62, 1.23, and 11.89 mg m^{-3}, respectively), with the latter being an exceptionally high reading. Notably, January and February had high

Tabla 2. *Opeatostoma pseudodon* number of individuals by sampling date and site. Sexual proportion and its statistical significance are included (χ^2 with Yates correction). Site abbreviations according to Table 1.

Collecting date and (site)	Total	Males	Females	Male:Female proportion	$\chi 2$	*P*
2014						
24/Jan (Es)	55	36	19	1.89:1.00	4.65	0.03
21/Feb (Dm)	39	18	21	1.00:1.17	0.10	0.75
21/Mar (Ar)	23	09	14	1.00:1.56	0.70	0.40
25/Apr (PP)	14	06	08	1.00:1.33	0.07	0.79
23/May (ML)	41	17	24	1.00:1.41	0.88	0.35
15/Aug (PC)	03	02	01	2.00:1.00	0.00	1.00
24/Oct (PC)	20	10	10	1.00:1.00	0.05	0.82
28/Nov (PT)	96	58	38	1.53:1.00	3.76	0.05
21/Dec (Es)	44	32	12	2.67:1.00	8.20	0.00
2015						
30/Jan (PT)	62	29	33	1.00: 1.14	0.15	0.70
27/Mar (PP)	05	01	04	1.00:4.00	0.80	0.37
30/Abr (PP)	54	28	26	1.08:1.00	0.02	0.89
15/May (LM)	10	05	05	1.00:1.00	0.10	0.75
12/Jun (SA)	60	34	26	1.31:1.00	0.82	0.37
15/Jul (BA)	06	03	03	1.00:1.00	0.17	0.68
21/Aug (PP)	51	31	20	1.55:1.00	1.96	0.16
25/Sep (PP)	54	27	27	1.00:1.00	0.02	0.89
16/Oct (PP)	60	30	30	1.00:1.00	0.02	0.90
27/Nov (PP)	11	05	06	1.00:1.20	0.00	1.00
04/Dec (PP)	60	28	32	1.00:1.20	0.15	0.70
Total	768	409	359	1.14:1.00	3.13	0.08

Table 3. Characterization of gonadal development stages of *Opeatostoma pseudodon* females.

Stage 1: oogenesis (S1)	Occurrence of ovogonia and nucleated oocytes adhered to the follicle's walls; scarce yolk granules are observed.
Stage 2: vitellogenic maturation (S2)	Mature follicles are full; oocytes with a nucleus and nucleolus adhered to the follicle walls are distinguished. Yolk granules and scarce yolk platelets are observed.
Stage 3: maturity (S3)	Oocytes with a nucleus and nucleolus adhered to the follicle wall. A larger number of yolk granules and platelets is observed.
Stage 4: spawning (S4)	Few yolk platelets in the follicles with scarce oocytes; thin follicle walls; remnant oocytes presenting nucleus and some with nucleolus.
Stage 5: resting (S5)	Follicles are empty or with scarce oocytes adhered to the wall; phagocytes are present.

spawning frequencies of 80 and 60%, respectively. The lowest chlorophyll concentrations were recorded in July, October, and November (0.19, mg m^{-3}), with July being the month when the highest frequency (70%) of resting females (S5) was registered (Fig. 4). An extraordinary value of chlorophyll was observed in April accompanied by 50% of resting (S5) and spawning (S4) reproductive phases.

Males

During 2014, the Chl-*a* concentration maxima coincided with the spawning (S3) frequency peaks observed in January, February, and December (60, 55, and 70%, respectively). In July, low chlorophyll concentrations corresponded to a 100% frequency for the resting gonadal phase (S4, Fig. 5).

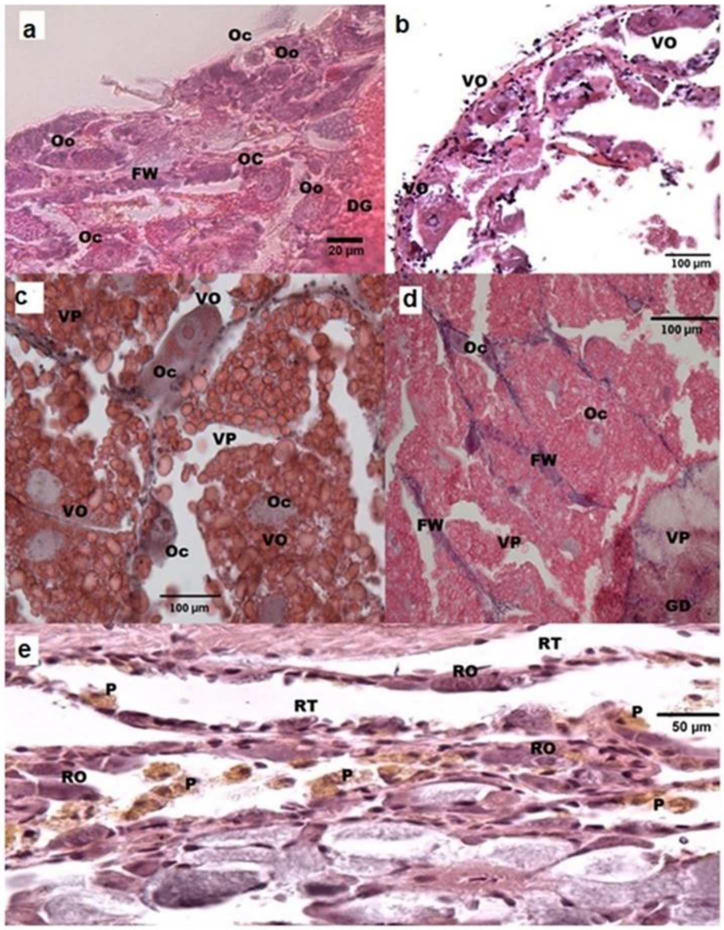

Figure 2. Histological sections of female *Opeatostoma pseudodon* showing ovarian stages: a) oogenesis, b) vitellogenic maturity, c) maturation, d) spawning, e) resting. Oo: oogonia, Oc: oocytes, DG: digestive gland, CT: connective tissue, VP: vitelline platelets, PvO: previtellogenic oocytes, VO: vitellogenic oocytes, FW: follicular wall, RO: residual oocytes, P: phagocytes, RT: resting tubules.

Table 4. Characterization of gonadal development stages of *Opeatostoma pseudodon* males.

Stage 1: spermatogenesis (S1)	Follicles with a greater number of spermatogonia, spermatids, and few spermatozoids.
Stage 2: maturity (S2)	Follicles are mainly filled with spermatozoids oriented towards the lumen and a lesser quantity of spermatogonia, spermatocytes, and spermatids.
Stage 3: spawning (S3)	Follicles are full of spermatozoids in expulsion oriented towards the lumen.
Stage 4: rest (S4)	Empty follicle lumen; folded ciliated columnar epithelium; resting tubules.

In 2015, high chlorophyll concentrations corresponded to high spawning (S3) frequencies registered in January (80%), February (55%) and December (70%, Fig. 5). As with females, the low Chl-*a* concentration in July coincided with a high percentage (70%) of individuals in the resting reproductive phase (S4, Fig. 5).

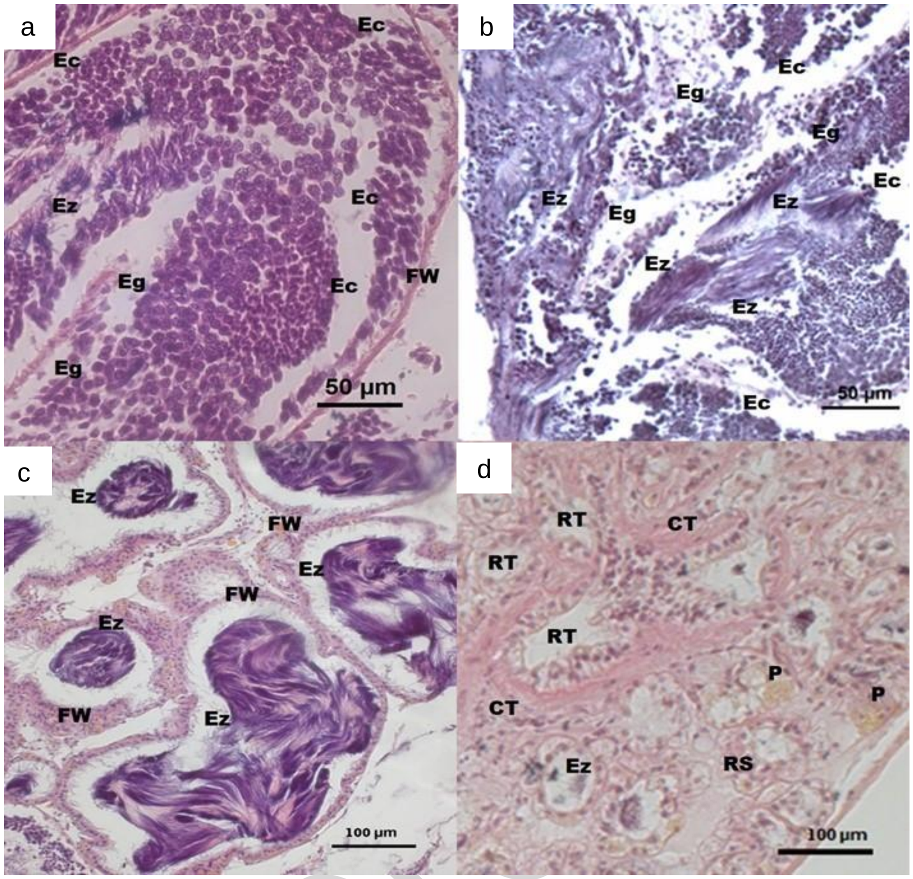

Figure 3. Histological sections of *Opeatostoma pseudodon* males showing testis stages: a) spermatogenesis, b) maturity, c) spawning, d) rest. Eg: spermatogonia, Ec: spermatocytes, Ez: spermatozoa, RS: residual spermatozoa, DG: digestive gland, CT: connective tissue, FW: follicular wall, P: phagocytes, RT: resting tubules.

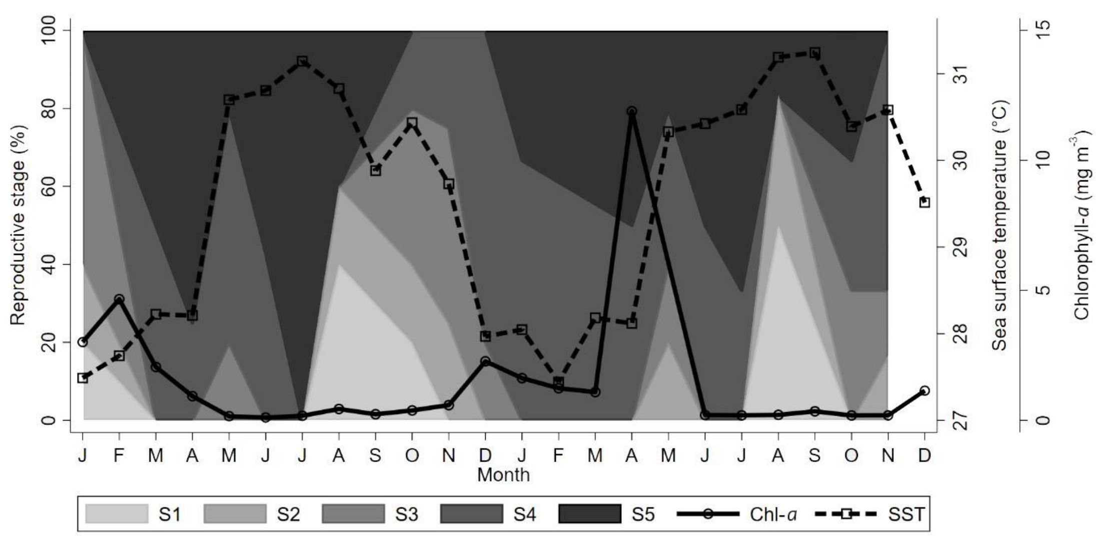

Figure 4. Frequency of gonadal stages 2014-2015 for *Opeatostoma pseudodon* females by sampling date. Chlorophyll-*a* (Chl- *a*) concentration (mg m^{-3}) and sea surface temperature (SST; °C) values are shown.

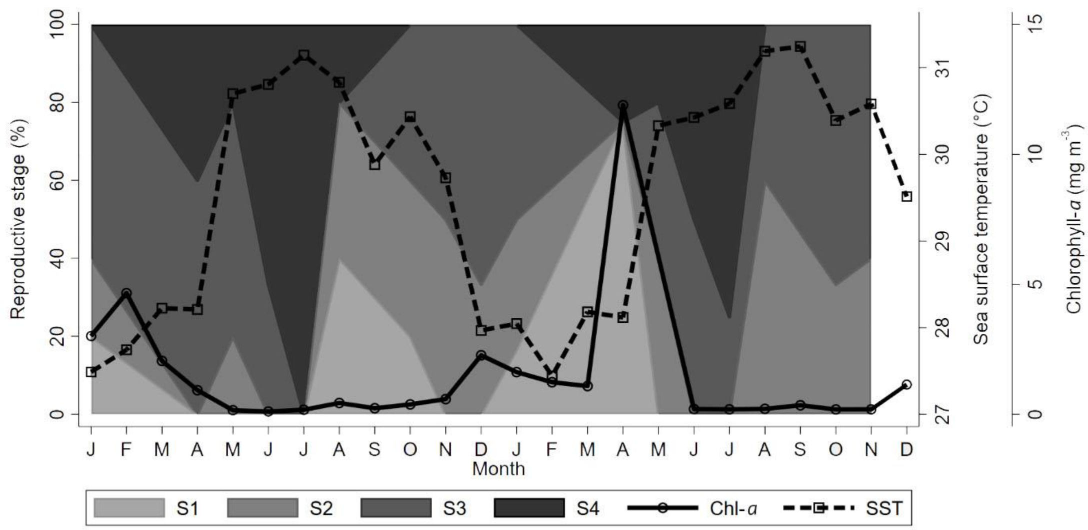

Figure 5. Frequency of gonadal stages 2014-2015 for *Opeatostoma pseudodon* males by sampling date. Chlorophyll-*a* (Chl-*a*) concentration (mg m^{-3}) and sea surface temperature (SST; °C) values are shown.

Temperature and gonadal cycle

Females

Higher temperatures were recorded in May 2014 (30.7°C), June 2014 (30.8°C), July 2014 (31.1°C), and August 2014 (30.8°C). These temperatures are associated with the months that have higher frequencies of gonadal rest (S5) (Fig. 4), particularly in July, when the frequency reached 100%. The lower recorded temperatures occurred in January (27.4°C), February (27.7°C), and December (27.9°C). The highest frequencies of the spawning stage (S4) were observed in December (80%) and January (60%). In April, the water temperature was 28.2°C with a peak of 70% of the resting stage (S4), and in May, when the temperature increased to 30.8°C, the spawning stage (S4) presented a high frequency value (60%).

In 2015, higher temperatures were registered in July (38.6°C), August (31.2°C), and September (31.4°C). July presented the maximum frequency (70%) of the resting stage (S5). Lower temperatures occurred in January (27.5°C), February (27.7°C), and December (27.9°C). These months had high frequencies of the spawning stage (S4) (70, 60, and 55%, respectively). In April, with a water temperature of 28.1°C, the spawning (S4) and resting (S5) stages had the same frequency (50%).

Males

July was the month with the highest frequency of resting stage (S4) (100%) (Fig. 5). High frequencies of spawning stage (S3) were registered in January (60%), February (55%), and December (80%). In April, 70% of the spawning stage (S3) and 30% of the resting stage (S4) occurred.

In July 2015, the resting stage (S4) was observed with a higher frequency (70%) (Fig. 5). On the other hand, the maturation and spawning stages (S2 and S3) had high frequencies in August (40 and 60%) and September (50 and 50%). Low temperatures corre-sponded to the spawning stage (S3) in January, February, and March (Fig. 5).

Smoothing and cross-correlation

To describe the variations and relationships between the reproductive stages and environmental measures (sea surface temperature and Chl-*a* concentration) during the study period in more detail, the smoothed reproductive stage frequencies were cross-correlated with temperature and concentration values. It can be seen (Fig. 6) that during the cooler months of the year (September to January), females mature (S3) and spawn (S4) shortly after October and until March. During 2015, it was observed that the spawning stage exhibited higher frequencies than the same period in 2014. Very clearly, females are in the resting stage (S5) during the warm half of the year (April to August). Cross-correlation of the data sequences reveals a slight desynchronization, with first maturation (S3) and then spawning (S4), and a four-month lag between spawning (S4) and resting (S5).

Males appear to mature slightly earlier than females, from August to January (Fig. 7). Spawning males (S3) were registered from September to February. As females, males are in the resting stage (S4) from April to August, during the warm months of the year.

Cross-correlograms for female stages (Fig. 6) reveal a three-month desynchronization between maturity-spawning (S3-S4) and spawning-resting (S4-S5) stages. For the males, there is a monthly lag between maturation (S2) and spawning (S3) and a four-month lag between spawning (S3) and resting (S4) (Fig. 7, Table 5).

Spawning females (S4) and males (S3) both exhibit a six-month desynchronization (lag = 6) with sea surface temperature (SST), but a synchronous variation with Chl-*a* concentration (lag = 0). Resting females (S5) and males (S4) exhibited lags of 3 and 2 months, respectively, with SST, and lags of -3 and -4 months with chlorophyll concentration (Table 5).

DISCUSSION

The total sex ratio of *O. pseudodon* from Puerto Ángel was found to be slightly biased towards the males ($P < 0.10$). However, an interesting pattern could be noticed when comparing monthly. Male individuals were more abundant during the warm part of the year (June-August) until the onset of the reproductive period (with a peak in February-March), when female individuals became dominant. This tendency could be due to a possible female gregarious behavior for oviposition, as observed with other marine gastropods (Elhasni et al. 2013).

Histological examination of the gonads allowed characterization of the gonadal cycle of *O. pseudodon* from Puerto Ángel, Oaxaca. Females showed five stages: initial oogenesis, vitellogenic maturation, maturity, spawning, and rest, while males showed only four stages: spermatogenesis, maturity, spawning, and rest.

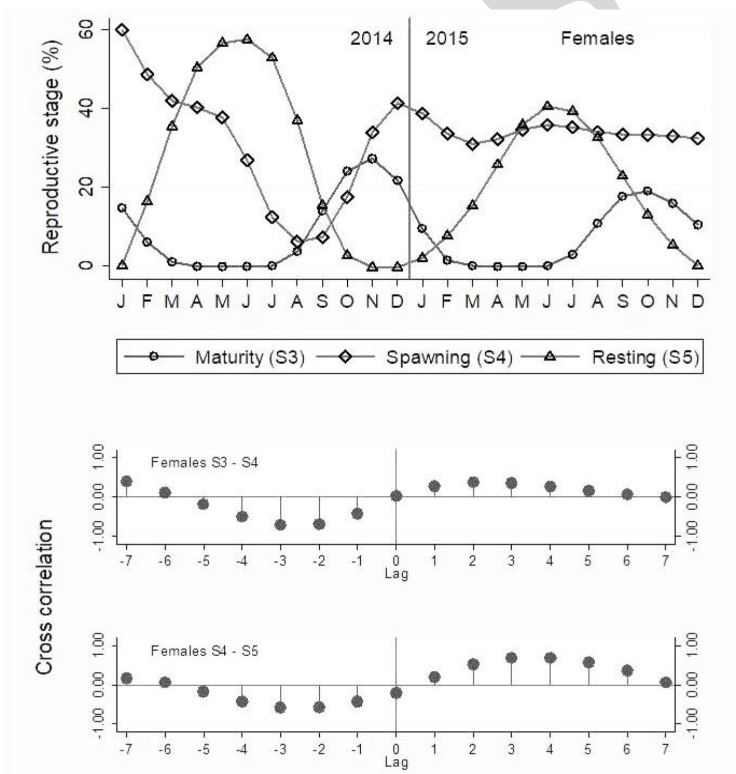

Figure 6. Smoothed frequency of female reproductive stages along the study period and cross-correlation correlograms for mature-spawning (S3-S4) and spawning-resting (S4-S5) reproductive stages.

Cross-correlation of the smoothed frequencies of the stage periods revealed that females take longer (three months) than males (one month) to achieve maturity. However, after spawning, males enter a rest period that is one month longer (four months) than females (three months).

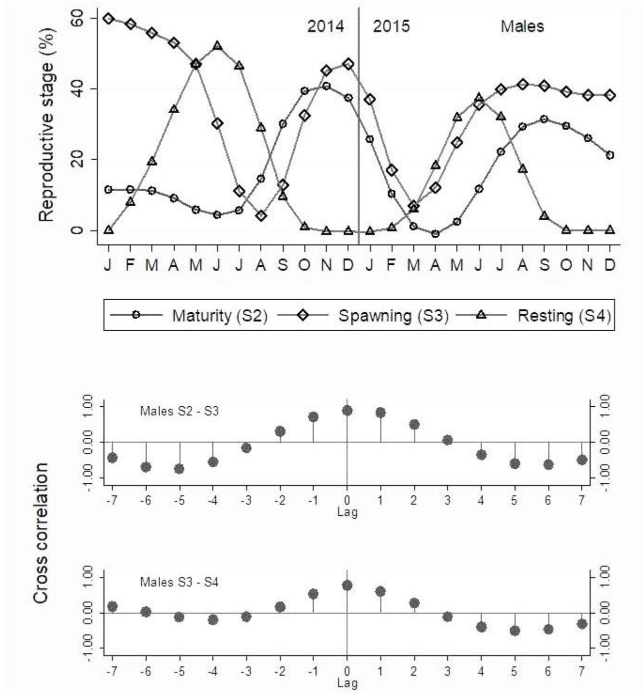

Figure 7. Smoothed frequency of male reproductive stages along the study period and cross-correlation correlograms for mature-spawning (S2-S3) and spawning-resting (S3-S4) reproductive stages.

Table 5. Cross correlation between reproductive stages and environmental (sea surface temperatures and chlorophyll-*a* concentrations): sex, sequences compared, monthly time lag, cross correlation, and statistical significance (*P*-values).

Sex	Sequence	Lag	Cross-correlation	*P*-value
Females	S3-S4	3	0.68	0.00
	S4-S5	3	0.79	0.00
Males	S2-S3	1	0.43	0.03
	S3-S4	4	0.62	0.00
Females	S4-SST	6	0.73	0.00
	S4-CL	0	0.68	0.00
Males	S3-SST	6	0.36	0.03
	S3-CL	0	0.50	0.02
Females	S5-SST	3	0.69	0.00
	S5-CL	-3	0.73	0.00
Males	S4-SST	2	0.66	0.00
	S4-CL	-4	0.84	0.00

Chlorophyll concentration, as an indicator of food availability (Hurtado et al. 2012), is indirectly related to the energy-demanding gonad development because it depends on the ingested food obtained from the environment or body reserves accumulated during periods of abundance (Mackie 1984, Park et al. 2011). *O. pseudodon* is a predator gastropod (Vermeij 2001); thus, it depends on its prey, which in turn obtains energy from lower levels of the trophic web. During the winter months (November-February), "Tehuanos" (Steenburg et al. 1998, Velázquez-Muñoz et al. 2011, González-Tejadilla 2018) winds blow from the north over the Gulf of Tehuantepec and its surroundings, causing outwellings of nutrient-rich bottom waters and phytoplankton blooms, which then provide abundant food for all consumers in the local ecosystem. From January to April 2014, Chl-*a* concentrations were high, coinciding with a high frequency of mature *O. pseudodon*

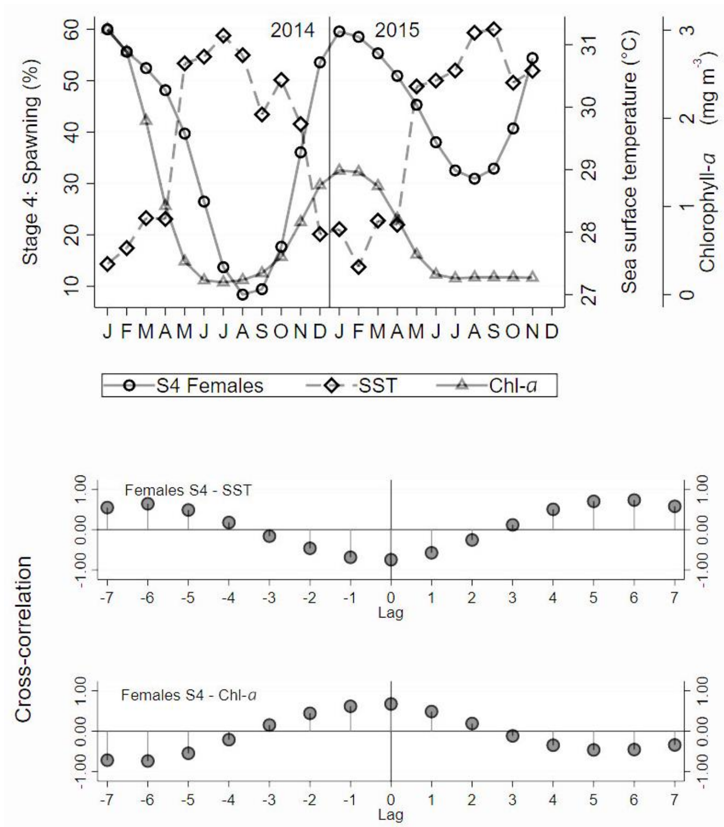

Figure 8. Smoothed frequency of spawning (S4) females, sea surface temperature (SST), and chlorophyll-*a* concentration (Chl-*a*) along the study period and cross-correlation correlograms for S4-SST and S4-Chl-*a*.

organisms. The relationship was clearer from October 2014 to April 2015, with synchronous high cross-correlation between the frequencies of mature organisms (S4 females, S3 males) and high Chl-*a* concentration values. It is possible that, due to the anomalously elevated Chl-*a* concentration measured in April 2015, the proportion of mature organisms remained relatively high for a longer period than in the previous year (Table 4, Figs. 9-10). It was observed that elevated Chl-*a* concentrations coincided with maturity stages indicative of gonad development, suggesting an ecological programming of hatching that occurs when high amounts of phytoplankton food are present in the aquatic environment, thereby ensuring a better survival probability for the offspring (Varpe et al. 2007, Avaca et al. 2015). Thus, it seems that, in a similar way to other sympatric gastropod species (*Hexaplex princeps*, Saito-Quezada et al. 2018), food availability is the main factor triggering the onset of *O. pseudodon* reproduction in this region.

Temperature is a key environmental factor influencing the reproductive cycle of mollusks (Mackie 1984, Collin & Ochoa 2016). In this study of *O. pseudodon*, both male and female cross-correlation values showed synchronous spawning stage frequency peaks lagged 6 months behind SST peaks. Therefore, there is significant statistical evidence that reproduction occurs during the cool months of the year. The resting stages last 3 (females) to 2 (males) months to coincide with temperature peaks during the warmer months.

To compare the reproductive cycle of *O. pseudodon* with that of other Mexican gastropod species, we considered the numerical data reported by Baqueiro et al. (2003). The percentages of spawned individuals were subjected to the same smoothing procedure (to recover the main patterns) as ours, and the results, along with those obtained by Saito-Quezada et al. (2018) and the data from this study, are presented (Fig. 12). It can be observed that four species, *Hexaplex erythrostomus* and *Strombus pugilis*, from Conception Bay and *Melongena corona* (Campeche Bay) and *Strombus gigas* (Chinchorro reef and Alacranes reef), spawn during the warm periods of the year. Only *Strombus gracilior* and *Fasciolaria tulipa* from Conception Bay,

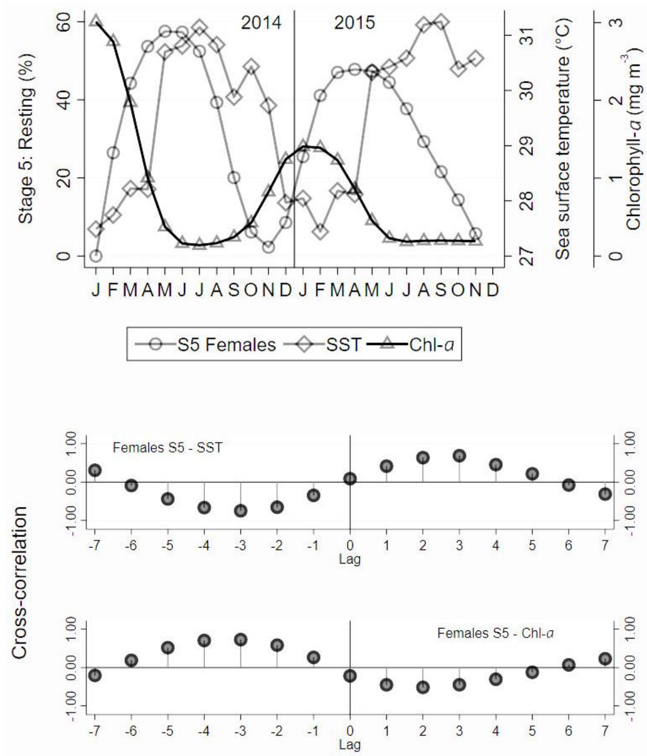

Figure 9. Smoothed frequency of resting (S5) females, sea surface temperature (SST), and chlorophyll-*a* concentration (Chl-*a*) along the study period and cross-correlation correlograms for S5-SST and S5-Chl-*a*.

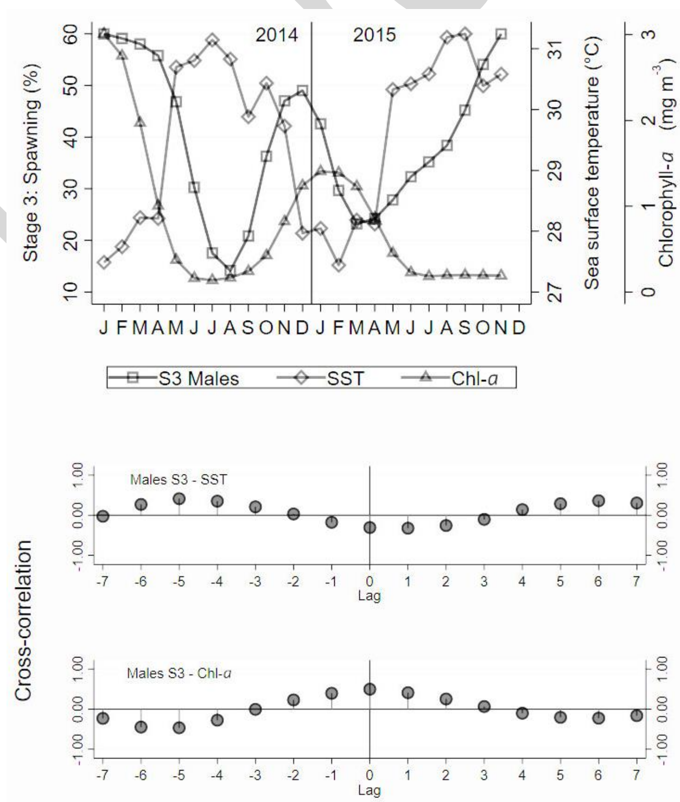

Figure 10. Smoothed frequency of spawning (S3) males, sea surface temperature (SST), and chlorophyll-*a* concentration (Chl-*a*) along the study period and cross-correlation correlograms for S3-SST and S3-Chl-*a*.

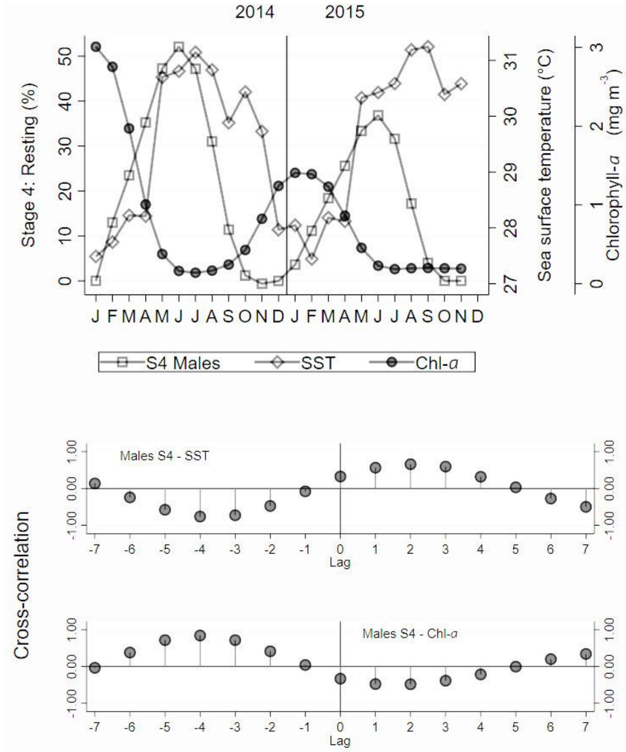

Figure 11. Smoothed frequency of resting (S4) males, sea surface temperature (SST), and chlorophyll-*a* concentration (Chl-*a*) along the study period and cross-correlation correlograms for S4-SST and S4-Chl-*a*.

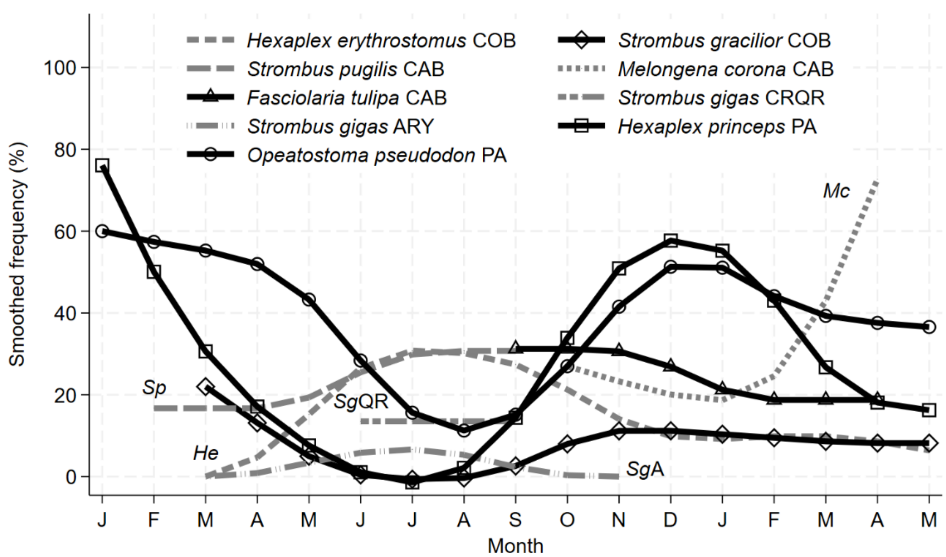

Figure 12. Graphical comparison of several gastropod species' spawn period from Mexican littoral waters. COB: Conception Bay; CAB: Campeche Bank, CRQR: Chinchorros reef, Quintana Roo, ARY: Alacranes Reef, Yucatán, PA: Puerto Ángel, Oaxaca. Sp*: Strombus pugilis*; *Mc: Melongena corona*; *Sg*QR*: Strombus gigas*, Quintana Roo; *He*: *Hexaplex erythrostomus*; SgA: *Strombus gigas*, Alacranes Reef; *O. pseudodon* spawn pattern and those similar are represented by continuous bold lines.

and *Hexaplex princeps* from Puerto Angel, have a spawning period during the coolest months of the year.

O. pseudodon partially corresponds to the patterns reported by Aldana-Aranda (2003), as having gametogenesis (spring and summer), one spawning pulse in the winter months, and a recovery period during spring-autumn months.

Finally, it can be stated that *O. pseudodon* matures and spawns during the cold months of the year (October to March) and rests its reproduction during the warm part of the year (May to August). The present study is the first to investigate the reproductive cycle of *O. pseudodon* in the region, providing baseline information for proposing management measures (such as avoiding captures during the reproductive peak in winter months) and assessing its aquaculture potential. To achieve these goals, further research is necessary. Additional information on reproductive aspects (median maturity size), relative and individual growth will be provided in further contributions.

Credit author contribution

V.M. Saito-Quezada: conceptualization, investigation, methodology, formal analysis, validation, writing-original draft, review and editing; E. Uría-Galicia: methodology, supervision, validation, visualization; J.L. Gómez-Márquez: resources, supervision, writing-original draft; A.B. Villaseñor-Martínez: methodology, supervision, writing-original draft; Ma. de L. Jiménez-Badillo: supervision, writing-original draft; L.E. Sanvicente-Añorve: methodology, validation; I.H. Salgado-Ugarte; conceptualization, data curation, formal analysis, funding acquisition, software, writing-original draft, review and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

AKNOWLEDGMENTS

We express our gratitude to the Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México (UNAM), and the former Consejo Nacional de Ciencia y Tecnología (now Secretaría de Ciencia, Humanidades, Tecnología e Innovación, SECIHTI) for their support. Local divers Manolo Jarquín (†), Primitivo Herrera Ordóñez, and Captain "Beto" (Abraham Reyes López) made the collection of specimens possible. Former students Mariana Evelyn Meléndez Contreras, Edgar Omar Guzmán Urieta, and Julio César Haro Capetillo assisted with specimen transportation and processing. We are grateful to Dra. Erika Rosales Cruz for her help with the histological photographs and to the Central de Instrumentación de Microscopía, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional. This research received support from Consejo Nacional de Ciencia y Tecnología (CVU: 215996; Scholarship: 207161) and the Dirección General de Asuntos del Personal Académico, UNAM, under the programs PAPIME (PE206213, PE207417, PE209120, PE204822, and PE206724) and partially PAPIIT (IG201215). Besides, we received support from the Carrera de Biología, Facultad de Estudios Superiores Zaragoza, UNAM. Lastly, we would like to thank all the students and colleagues of the Laboratorio de Biometría y Biología Pesquera at UNAM. The corrections and suggestions from three anonymous reviewers significantly improved the final manuscript version. We thank M.M. Salgado-Saito for the final edition of graphs.

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