Research Article

Reproductive cycle of *Calamus brachysomus* (Teleostei: Sparidae) in the Central Gulf of California, BCS, Mexico

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ABSTRACT. The Pacific porgy *Calamus brachysomus* (Lockington, 1880) is exploited for local consumption and commerce in Baja California Sur (BCS). Monthly samples to study its reproductive biology were obtained from the artisanal fishery operating in Santa Rosalía, BCS, Mexico, from July 2015 to July 2016. A total of 265 specimens were analyzed, including 147 females and 118 males. The sexual proportion (1.24F:1M) did not differ from the expected 1:1 proportion ($P = 0.08$). There were no significant differences between sexes in total length ($P = 0.94$). Variations in the hepatosomatic index and condition factor indicated that food constituted the main energy source during reproduction, with possible additional use of endogenous reserves originating in the liver during spawning. The gonads histological analysis indicated an asynchronous ovarian development and batch spawning strategy. There were spawning capable females during 11 of the 13 sampled months; the exceptions were February and September, coinciding with minimum and maximum sea surface temperature (SST) values. These results, along with the gonadosomatic index variations, allowed us to conclude that *C. brachysomus* reproduces over a large part of the year with an activity peak from May to July, in an SST interval of 21 to 28ºC.

Keywords: *Calamus brachysomus*; Sparidae; fishes; reproduction; gonad histology; morphophysiological indices

INTRODUCTION

Knowledge of biological aspects of commercially important fishes constitutes one of the main research objectives of fishery science worldwide (Lowerre-Barbieri et al. 2011). Within this context, the analysis of reproductive biology provides information on the sexual proportion of populations, the size at recruitment, the sexual pattern of the species, and the spawning period, among other topics (Heyman et al. 2019). Information garnered by reproductive studies constitutes a fundamental tool contributing to the effective management of fishery resources (Morgan 2008, Lowerre-Barbieri et al. 2018).

Teleost fishes of the family Sparidae present a wide distribution in tropical and temperate areas (Sheaves 2006). They have reproductive strategies such as gonochorism and simultaneous and sequential herma-phroditism (Sadovy & Liu 2008). They also display explay extended spawning seasons related to adequate environmental conditions for larval survival (Pavlidis & Mylonas 2011). The genus *Calamus* includes economically important species, most of which are exploited by fisheries, but knowledge of their biology is still scarce or inexistent (Tyler-Jedlund 2009). The only representative of the family Sparidae inhabiting the Gulf of California is the Pacific porgy *Calamus brachysomus* (Salas et al. 2011). This species is caught as bycatch in a multispecific fishery; however, it is generally accepted in national markets and is important in the commercial fisheries of coastal Baja California Sur (BCS), known by the common name of "mojarrón" or "mojarra mueluda." The Pacific porgy inhabits rocky reefs in the coastal area of Santa Rosalía, which is characterized by high fisheries activity.

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The increasing interest in *C. brachysomus* as a fishery resource and the scarce existing information on its biology led to the need to increase knowledge on this species. Therefore, the objective of the present study was to provide information on the reproductive biology of *C. brachysomus*, such as its reproductive cycle and the relationship between reproduction and sea surface temperature; we also analyzed body indices as indicators of reproduction and storage of reserve substances. Information on these aspects is a valuable contribution to developing management plans for the sustainable exploitation of this resource.

MATERIALS AND METHODS

Monthly sampling was undertaken from July 2015 to July 2016; Pacific porgy *Calamus brachysomus* specimens were collected from the commercial catches obtained by fishermen in the coastal area of Santa Rosalía, in the central area of the Baja California Peninsula, Mexico (Fig. 1). A total of 480 coastal fishery vessels measuring from 6.7 to 10 m in length operate in the area. *C. brachysomus* is caught along with species such as *Mycteroperca rosacea*, *Paralabrax auroguttatus*, and *Lutjanus guttatus* using 4-inch gillnets placed at between 10 and 35 m depth (Arce-Acosta 2015).

The total length (TL ± 0.1 cm) and total weight (TW ± 0.1 g) of each fish were recorded. Gonads were extracted, weighed (GW ± 0.1 g), and fixed in Davidson's AFA solution; they were then processed using a standard histological technique that Humason (1979) modified. Samples were dehydrated in solutions with increasing ethanol concentrations (80, 90, 96, and 100%), infiltrated with paraffin, cleared with xylene (inclusion core Arcadia H+C®), and embedded in Paraplast®. Four to 5-µm thick sections were obtained with a microtome (Leica® RM2025). Finally, tissues were stained with Harris hematoxylin-eosin (Multistainer Leica® ST5020) and analyzed using a vertical DM4B microscope with a Leica DMC2900 digital camera in the program Leica Application Suite (LAS).

Sex and phases of reproductive development were identified based on the analysis of histological sections of the gonads. The criteria proposed by Brown-Peterson et al. (2011) were used to identify gonad developmental phases, whereas oocyte developmental stages were determined according to Tyler & Sumpter (1996). Five histological cuts were performed for each gonad developmental stage per month to obtain oocyte diameters. Ten oocytes at each of the observed stages were measured per cut. Diameters were calculated as the average between the largest and smallest oocyte; only oocytes with visible nuclei were used (West 1990).

To assess the physiological condition of individuals, we used the following somatic indices: gonadosomatic index (GSI), calculated with the equation proposed by Mouine et al. (2007) GSI = [GW / EWS] × 100 (GW: gonad weight; EWS: eviscerated weight of the specimen); hepatosomatic index (HSI), calculated as HSI = [LW / EWS] × 100 (LW: liver weight) (Anderson & Gutreuter 1983); and condition factor (Kn) (Le Cren 1951), calculated as Kn = W' / W × 100 (W': the estimated weight for each length value, obtained from the weight-length relationship $\left(W = a\ TL^b\right)$; W: observed weight). The reproductive cycle was assessed based on the relative frequencies of the gonadal developmental phases obtained monthly and GSI values.

During the study period, sea surface temperature (SST) values were obtained from satellite images downloaded from the Scripps Institution of Oceanography (https://scripps.ucsd.edu/). These images were processed with the Windows Image Manager© software (WIMSoft).

Chi-squared tests with Yates' correction were used to analyze the size structure and sexual proportion. The monthly variation in morphological indices by sex was analyzed with Kruskal-Wallis tests and multiple Dunn comparisons (Sokal & Rohlf 2012). The average total length of males and females and the condition index values between sexes were evaluated using a Mann-Whitney test. Spearman rank correlation tests evaluated possible relationships between GSI, HSI, and Kn in males and females. The level of significance established for all statistical analyses was 0.05 (Sokal & Rohlf 2012). Statistical analyses were performed with IBM SPSS Statistics 21 software.

RESULTS

Size composition and sexual proportion

A total of 265 specimens were collected, of which 147 (55%) were females, and 118 (45%) were males (Table 1). Females measured between 16.5 and 36.5 cm TL (mean ± standard deviation, 24.5 ± 3 cm), and males measured between 15 and 37 cm TL (24 ± 3.1 cm). There were no significant differences between the sexes in average TL (z = -0.07, $P = 0.9$). The size-frequency distribution is shown (Fig. 2). The general sexual proportion (1.24F:1M) was not significantly different from the expected 1:1 proportion ($X^2 = 2.95$, $P = 0.08$). Average sizes and monthly sexual proportions are shown in Table 1.
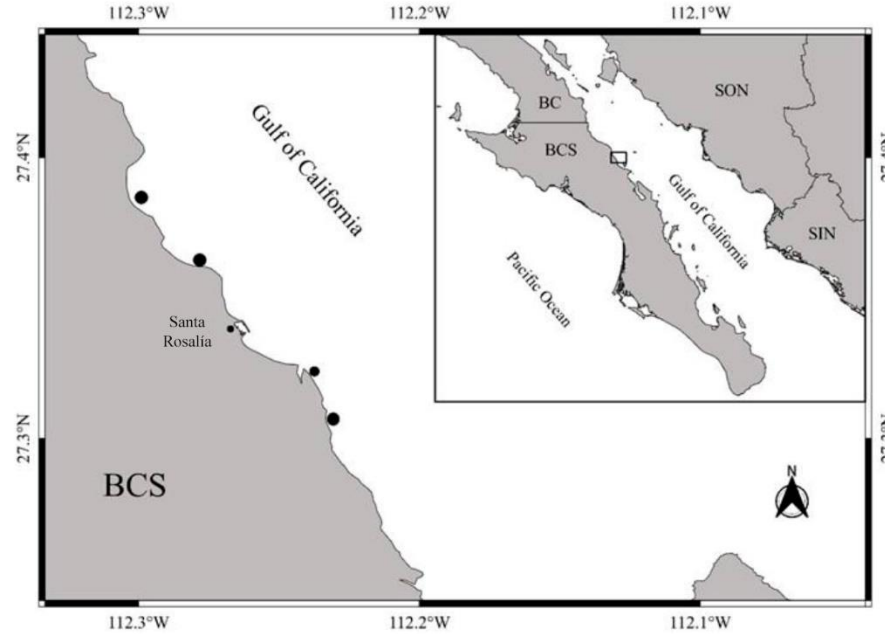
Figure 1. Area of study. The black dots show the capture sites of *Calamus brachysomus* in Santa Rosalía, Baja California Sur (BCS), Mexico.
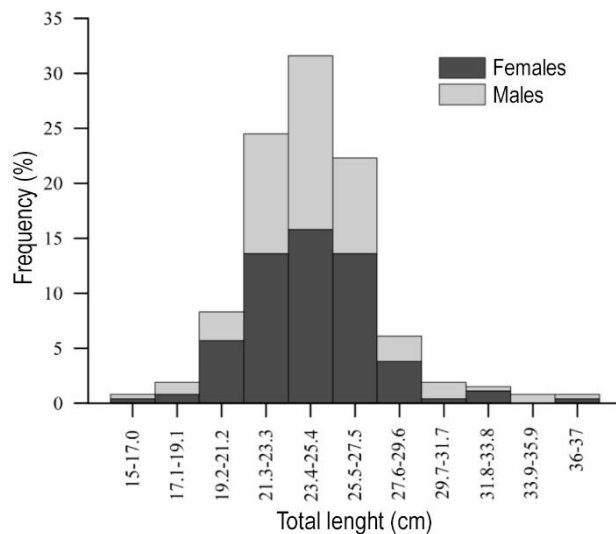

Figure 2. Sexual proportion of *Calamus brachysomus* by size interval in Santa Rosalía, Baja California Sur, Mexico, n = 265.

Monthly variation in the gonadosomatic index (GSI), hepatosomatic index (HIS), and condition factor (Kn)

GSI differed significantly between months for females ($H_{13,147}$ = 75.12. P = 0.001) and males ($H_{13,118}$ = 58.91, P = 0.001). The highest GSI values were recorded from April to July 2016, and the maximum value was obtained in May (3.11 for females and 2.7 for males) (Figs. 3a-b). There was a marked variability in HSI

values during the year for females ($H_{13,147}$ = 39.67, P = 0.001) and males ($H_{13,118}$ = 35.26, P = 0.001). The index ranged from 0.28 to 1.07 in females and 0.24 to 0.79 in males (Fig. 3c-d). The Kn was stable for both sexes during the analyzed period, with variations between 0.8 and 1 in males and females. There were no significant differences between months in the Kn for females ($H_{13,147}$ = 14.04, P = 2.98) and males ($H_{13,118}$ = 19.11, P = 0.06) (Figs. 3e-f). The GSI (Z =-3.9, P = 0.001) and HSI (Z =-2.4, P = 0.015) were significantly different between sexes; on the other hand, the Kn was not significantly different between sexes (Z=-1.21, P = 0.22).

A correlation analysis of the three indices by sex showed that in females the GSI and HSI were positively correlated (r_s = 0.30, P = 0.00), but the Kn was not significantly correlated with the GSI (r_s = 0.12, P = 0.13) or the HSI (r_s = 0.09, P = 0.26). Likewise, there was a positive correlation between GSI and HSI (r_s = 0.339, P = 0.00) in males, but the Kn was not significantly correlated with the GSI (r_s = -0.076, P = 0.4) or the HSI (r_s = 0.065, P = 0.48).

Gonadal microstructure and reproductive development

Developing ovaries presented abundant oocytes at the chromatin nucleolus (35.7 ± 7.8), perinucleolus (54.3 ± 8.8), and cortical alveolus stages (179.9 ± 11.9) (Fig. 4a), in addition to vitellogenesis I (188.9 ± 28.1) and II (211.8 ± 33.2 µm). Gonads of mature specimens presen-

Table 1. Monthly average size and monthly sexual proportion with respective X^2 values for *Calamus brachysomus*. The asterisk indicates significant differences from a 1:1 proportion ($P < 0.05$). Year 15: 2015, year 16: 2016. SD: standard deviation.

| Month/Year	n	Females Total length (cm) (mean ± SD)	n	Males Total length (cm) (mean ± SD)	Total	Sexual proportion (F:M)	X^2
July/15	9	24.3 ± 2.6	12	24.5 ± 2.5	21	0.75:1.0	0.19
August/15	10	23.8 ± 3.3	9	25.1 ± 2.9	19	1.11:1.0	0.81
September/15	7	24.7 ± 3.8	8	25.0 ± 1.6	15	0.87:1.0	0.79
October/15	7	25.7 ± 2	15	23.0 ± 3.8	22	0.46:1.0	2.23
November/15	9	22.7 ± 1.2	4	23.6 ± 1.4	13	2.25:1.0	1.23
December/15	10	24.6 ± 2.2	5	24.5 ± 1.4	15	2:1.0	1.06
January/16	16	24.8 ± 1.6	6	27.1 ± 1.4	22	2.6:1.0	3.68
February/16	14	26.1 ± 4	8	24.2 ± 1.7	22	1.75:1.0	1.13
March/16	11	25.5 ± 3	12	25.6 ± 2.1	23	0.91:1.0	0.8
April/16	3	27.1 ± 5.3	9	26.9 ± 5.7	12	0.3:1.0	2.08
May/16	11	25.5 ± 2.5	8	25.4 ± 3.7	19	1.37:1.0	0.21
June/16	28	23.7 ± 3.4	14	23.3 ± 1.7	42	2:1.0	4.02*
July/16	12	23.6 ± 1.8	8	21.0 ± 1.6	20	1.5:1.0	0.45
Total	147	24.5 ± 3	118	24 ± 3.1	265	1.24:1.0	2.95
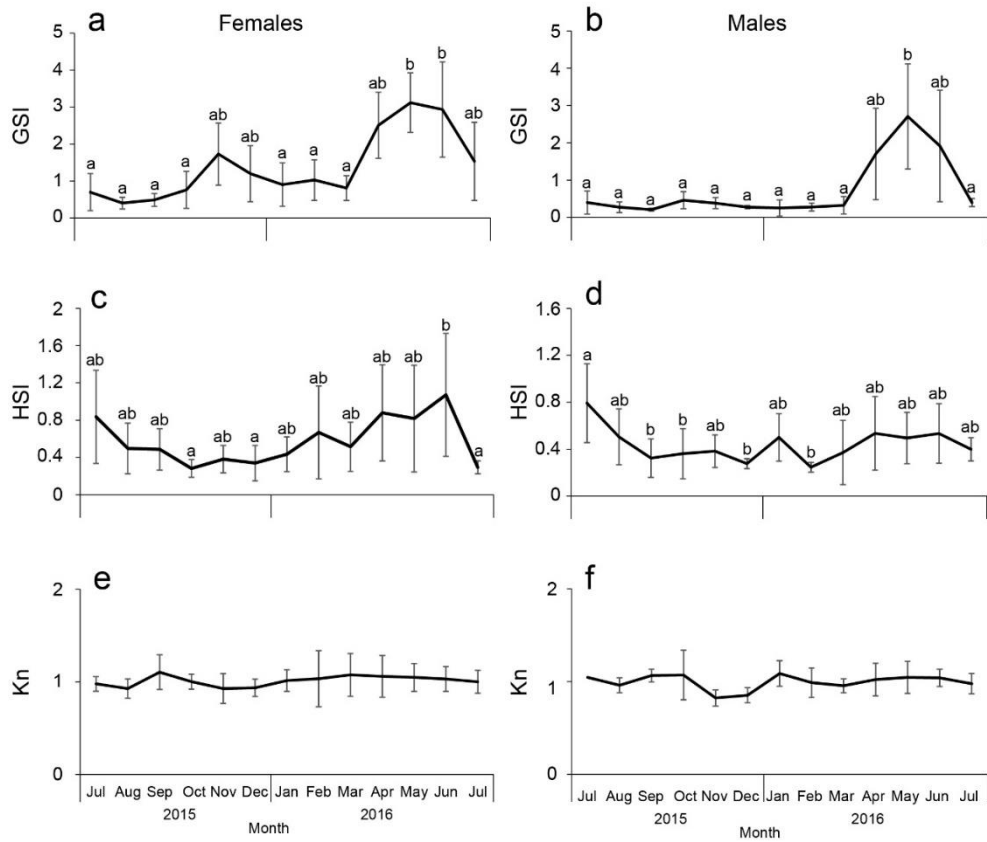
Figure 3. Monthly variation in the morphophysiological indices of *Calamus brachysomus* in Santa Rosalía, Baja California Sur, Mexico. a) Gonadosomatic index (GSI) in females, b) GSI in males, c) hepatosomatic index (HIS) in females, d) HIS in males, e) condition factor (Kn) in females, f) Kn in males. Different letters indicate significant differences ($P < 0.05$). Bars correspond to the standard deviation.
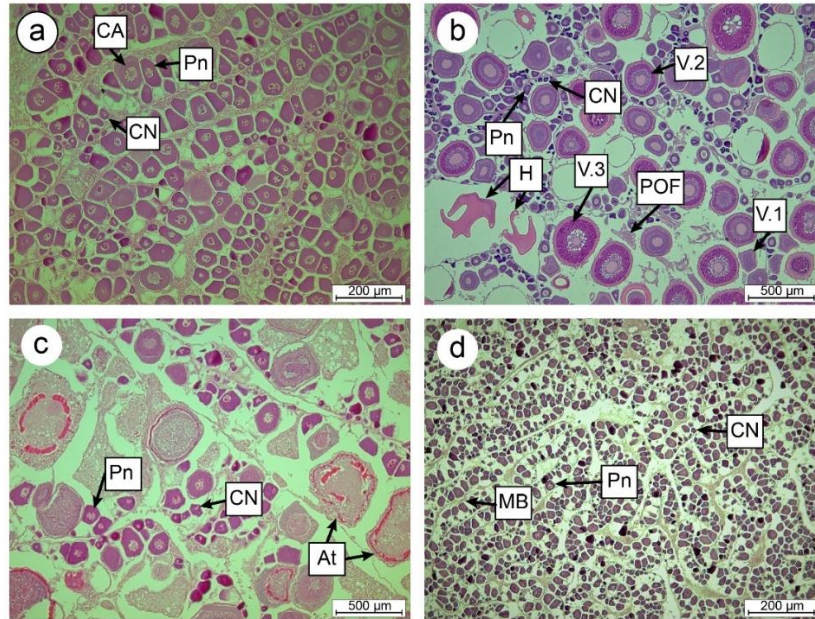
Figure 4. Transverse sections of the ovary of *Calamus brachysomus* at different phases of reproductive development. a) Developing ovary (CN: oocyte at chromatin nucleolus stage, Pn: oocyte at the perinucleolar stage, CA: cortical alveolus stage), b) ovary at the spawning capable phase (V.1, V.2, and V.3: vitellogenic oocytes 1, 2, and 3; H: hydrated oocyte; POF: postovulatory follicle), c) ovary in regression (At: atretic oocytes), d) ovary in regeneration (MB: muscular band).

ted, along with the previously mentioned stages, oocytes at vitellogenesis III ($335.8 \pm 40 \,\mu m$), germinal vesicle migration ($335.8 \pm 40 \,\mu m$), and hydrated oocytes ($474.12 \pm 77.6 \,\mu m$), as well as postovulatory oocytes, suggesting the occurrence of spawning before capture (Fig. 4b). The presence of oocytes at different stages of development, with no dominant type, indicated an asynchronous ovarian development. A total of 27 females presented germinal vesicle migration (GVM) and hydrated oocytes (H), indicating imminent spawning. One of these actively spawning females was found in December 2015, and the rest were found in March (1), April (1), May (4), June (13), and July (7). The simultaneous presence of GVM, H, and POF, together with oocytes at early and mid-vitellogenesis, allowed the identification of a batch spawning strategy. Gonads in regression were characterized by abundant atresias (Fig. 4c). Regenerating gonads only presented oocytes at the chromatin nucleolus and perinucleolus stages (Fig. 4d).

Spermatogenesis occurred in spermatic cysts distributed along the lobules. Spermatogonia appeared as isolated cells associated with Sertoli cells, scattered throughout the lobules. This testicular organization was indicative of an unrestricted lobular type. Testes of developing specimens presented spermatogonia, spermatocytes I and II, spermatids, and spermatozoids. Sper-matocytes I were the most abundant cell types; spermatozoids were observed only within spermatic cysts, whose lumen was still visible (Fig. 5a). Abundant spermatozoids were observed in the cysts and seminal ducts of mature specimens (Fig. 5b). Testes in regression presented abundant residual sperm, spermatocytes I, and connective tissue (Fig. 5b), whereas regenerating testes presented abundant spermatogonia and brown bodies (Fig. 5d).

Reproductive cycle and sea surface temperature (SST)

The monthly frequencies of the different gonadal developmental phases recorded for females and males are shown (Fig. 6). There were specimens in development and regeneration during the most analyzed months. Fish of both sexes were found at the regression phase from May to July 2016, whereas only males were found in regression from October to December and February. Spawning capable females were present during 11 of the 13 sampled months. The greatest frequencies of sexually active females were found in November (35%), December (40%), and from April to July (April = 21%, May = 100%, June = 60%, and July = 63%) (Fig. 6a). Spawning-capable males were found in October (7%), April (50%), May (50%), and June (30%) (Fig. 6b).
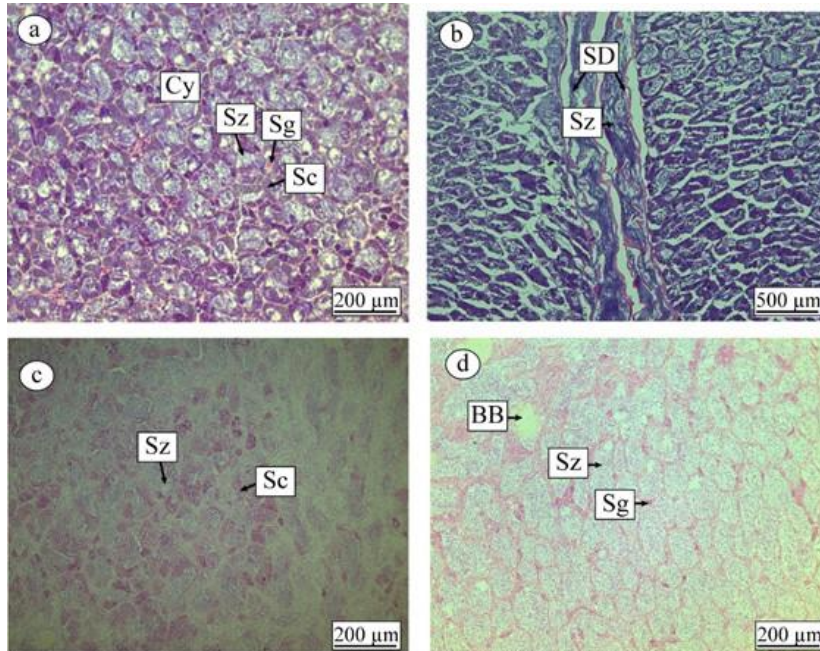
Figure 5. Transverse sections of the testis of *Calamus brachysomus* at different phases of reproductive development. a) Development, b) spawning capable, c) regression, d) regeneration. Cy: spermatic cyst, Sg: spermatogonia, Sc: spermatocytes, Sz: spermatozoa, SD: spermatic ducts, BB: brown body.

When the SST and reproductive cycle values were compared, we found individuals at the spawning capable phase at a temperature interval between 21 and 28°C. In contrast, most individuals at the regeneration phase were found at temperatures between 19 and 20°C and between 30 and 31°C.

DISCUSSION

The size range of specimens obtained in this study was 15 to 37 cm TL, similar to that obtained by Barr et al. (2003) in Colima (21 to 46 cm TL) and by Abitia-Cárdenas et al. (1990) in Bahía Concepción (20 to 33 cm TL). The sexual proportion was not significantly different from 1:1 when calculated for all specimens or by size intervals. Sexual distribution by size in sparids is usually associated with a sequential hermaphrodite sexual pattern (Pavlidis & Mylonas 2011). However, differences in this parameter are not always due to hermaphroditism and could also result from dimorphism in size and differential rhythms of growth and maturation (Sadovy-Shapiro 1987). These factors did not seem to influence the proportion of males and females in the Santa Rosalía population.

Although the GSI is an easily applied and interpreted tool in fish reproduction studies, its use needs to be validated with histological methods (De Vlaming et al. 1982). Most specimens found in the

regression phase corresponded to the minimum GSI values (<1) for both sexes in the present study. The greatest value of this index was recorded for fish at the spawning capable phase, which demonstrated that the use of GSI is adequate to monitor the reproductive development phases of this species.

Fishes can store reserve substances (usually glycogen, proteins, and lipids) in the liver, muscle, and adipose tissue to supply the energy required for the phases of gonad maturation (Alonso-Fernández & Saborido-Rey 2012). This strategy is common in fishes that decrease food consumption or stop ingesting food during reproduction (Saborido-Rey 2004). Other fishes, on the contrary, obtain the energy required by constantly feeding during the reproductive period (Alonso-Fernández & Saborido-Rey 2012). However, some species compensate for insufficient reserve storage or very extensive spawning periods with a mix of the two strategies (Aristizabal 2007). One way to infer energetic spending and the strategy used during reproduction is to monitor variations in muscle weight, liver weight, and quantity of accumulated fat. The HSI temporal trend was similar to the GSI for both sexes, suggesting the storage of energetic reserves in the liver during spawning. Despite the significant correlation between these indices, we found a low coefficient of determination, which could indicate short-term periods of energy storage (González & Oyarzún 2003). The
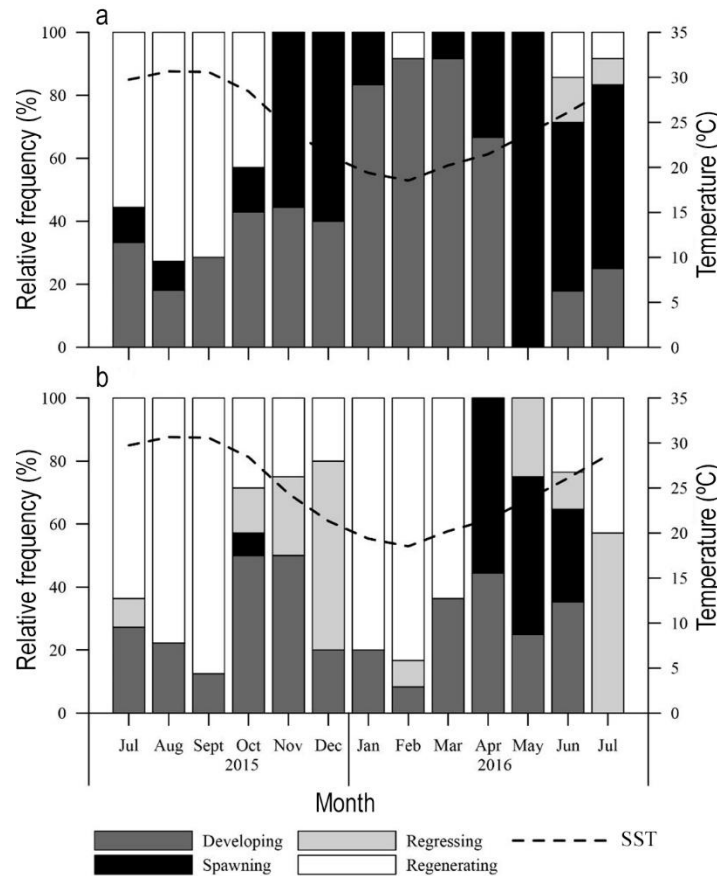
Figure 6. Reproductive development of *Calamus brachysomus* in Santa Rosalía, Baja California Sur, Mexico throughout an annual cycle. a) Females, b) males. The dotted lines represent the SST monthly mean concerning the reproductive cycle.

HSI of males was lower than that of females during the reproductive peak; this could be due to the lower energetic investment that the production of sperm entails in some species (Al Mamry et al. 2009).

There was marked temporal stability of Kn in both sexes, which indicates that the Pacific porgy *Calamus brachysomus* did not use reserves from muscle for reproduction. Based on the temporal trend of the somatic indices, we suggest that food constituted the main source of energy used for reproduction in *C. brachysomus*. However, there is a possibility that additional energetic reserves from the liver that were used during spawning cannot be discarded.

A similar pattern for the somatic indices analyzed in our study has been described for other members of the Sparidae family, such as *Pagellus erythrinus* and *Dentex dentex* (Ben-Smida et al. 2014, Grau et al. 2016). This independence from endogenous energy for gamete production is usually found in species that feed year-round, keeping a continuous energy input even during reproduction (González 2001). However, exten-

ded spawning periods imply important energetic spending (Lambert & Dutil 1997), increasing energy consumption, and other activities such as mating behavior (Brawn 1961). According to Adams et al. (1982), the use of endogenous energy is necessary when the required energy is not covered by food, which would explain the similar trends between GSI and HSI observed in this study.

Oogenesis in *C. brachysomus* was evidenced as a continuous process, characterized by the presence of primary growth oocytes, cortical alveoli oocytes, and vitellogenic oocytes in mature specimens, without a predominant stage, indicating an asynchronous ovarian development and a batch spawning strategy (Murua & Saborido-Rey 2003), which is common in the members of Sparidae (Pavlidis & Mylonas 2011). Three types of testicular development have been described in teleosts: tubular, restricted lobular, and unrestricted lobular (Uribe et al. 2014). According to the testicular organization and gametogenic cell arrangement, *C. brachysomus* presented unrestricted lobular testes, characterized by lobules with germinal epithelium

ending in dead ends towards the periphery of the testes and by spermatogonia distributed along the length of the lobules and not confined to the periphery. This type of morphological organization of the testes has been previously reported in other members of the family, such as *Archosargus probatocephalus* and *Acanthopagrus schlegelii* (Grier et al. 1980, Gwo & Gwo 1993).

The reproductive cycle of the Pacific porgy comprised four phases: development, spawning capable, regression, and regeneration. The presence of hydrated oocytes in fish histological sections is not common due to their collapse during the histological processing because hydrated oocytes appear approximately 24 h or less before spawning (Brown-Peterson et al. 2011). In the present study, 27 females presented hydrated oocytes, which indicated the spawning season and that the species spawned in the area.

Based on the GSI analysis, the reproductive development, and presence of spawning capable females during 11 of the 13 analyzed months, we infer that the Pacific porgy can reproduce year-round. However, there were two peaks in reproductive activity, from November to December and from May to July, with the highest GSI values for both sexes and the greatest abundance of fish at the spawning capable phase during the latter period. These results are similar to those reported by Avendaño-Ibarra et al. (2004), who found *C. brachysomus* larvae from March to December 1997 in Magdalena Bay greatest number of abundances from November to June. Additionally, Druzhinin (1974) found Pacific porgy spawning capable females in November and June off the coast of Peru.

The exogenous variables influencing reproduction are temperature, photoperiod, precipitation, quantity and quality of the food, and predation (Pavlidis & Mylonas 2011). Among these, the temperature has stood out due to its role as a stimulus for the beginning of final maturation, ovulation, and duration of spawning (Sarre & Potter 1999, Pankhurst & Porter 2003). Dubovitsky (1977) reported that spawning by *Calamus prioridens* was temperature-dependent in the Campeche Bank, Mexico and that temperature influenced the productivity of plankton in the area. Most individuals capable of spawning were found in a temperature range between 21 and 28ºC. In agreement with our results, it has been reported that *C. brachyosmus* larvae occur in Magdalena Bay year-round, with the greatest abundances in a temperature interval between 21.0 and 25.5ºC (Avendaño-Ibarra et al. 2004, Leal-Espinoza 2006). Additionally, Matus-Nivón et al. (1989) found Pacific porgy eggs in spring and summer at temperatures between 20 and 26ºC at Espiritu Santo Island.

It has been determined that *Calamus leucosteus*, *C. nodosus*, and *C. prioridens* present protogynous hermaphroditism. This sexual pattern is characterized by a bimodal size distribution, significant differences in sexual proportion, and histological evidence of individuals in sexual transition (Waltz et al. 1982, Horvath et al. 1990, Tyler-Jedlund 2009). For *C. brachysomus*, our findings showed no significant differences in sex ratios both for the whole fish sample and within different size intervals. In addition, the general size distribution did not show a bimodal trend, and there was no histological evidence of hermaphroditism or bisexuality. These results suggest a gonochoric sexual pattern. However, given the sexual complexity characterizing sparids, we recommend that the sample size be increased and the range of analyzed sizes for studies of sexual pattern determination, including immature individuals, which were not registered in the present study, constituting a bias attributed to the fact that samples were obtained from artisanal fisheries.

REFERENCES

Abitia-Cárdenas, L.A., Rodríguez-Romero, J. & Galván-Magaña, F. 1990. Observación trófica de tres especies de peces de importancia comercial en la Bahía Concepción Baja California Sur, México. Investigaciones Marinas, CICIMAR, 5: 55-61.

Arce-Acosta, M. 2015. Interacciones entre pesquerías ribereñas en el corredor Santa Rosalía-Mulegé, Baja California Sur, México. Tesis de Magíster en Ciencias, Centro Interdisciplinario de Ciencias Marinas, La Paz.

Adams, S.M., McLean, R.B. & Parrotta, J.A. 1982. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. Transactions of the American Fisheries Society, 111: 549-558.

Al Mamry, J.M., McCarthy, I.D., Richardson, C.A. & Meriem, S.B. 2009. Biology of the kingsoldier bream

(*Argyrops spinifer*, Forsskal 1775; Sparidae), from the Arabian Sea, Oman. Journal of Applied Ichthyology, 25: 559-564.

Alonso-Fernández, A. & Saborido-Rey, F. 2012. Relationship between energy allocation and reproductive strategy in *Trisopterus luscus* (Gadidae). Journal of Experimental Marine Biology and Ecology, 416: 8-16.

Anderson, R.O. & Gutreuter, S.J. 1983. Length, weight and associated structural indices. In: Nielsen, L. & Johnson, D. (Eds.). Fisheries techniques. American Fisheries Society, Maryland, pp. 283-300.

Aristizabal, E.O. 2007. Energy investment in the annual reproduction cycle of female red porgy, *Pagrus pagrus* (L.). Marine Biology, 152: 713-724.

Avendaño-Ibarra, R., Funes-Rodríguez, R., Hinojosa-Medina, A., González-Armas, R. & Aceves-Medina, G. 2004. Seasonal abundance of fish larvae in a subtropical lagoon in the west coast of the Baja California Peninsula. Estuarine Costal and Shelf Science, 61: 125-135.

Barr, E.E., Romero, M.C. & Boa, A.G. 2003. Peces marinos con valor comercial en la costa de Colima. Comisión Nacional para el Uso y Conocimiento de la Biodiversidad. Instituto Nacional de la Pesca, Ciudad de México.

Ben-Smida, M.A., Hadhri, N., Bolje, A., El-Cafsi, M. & Fehri-Bedoui, R. 2014. Reproductive cycle and size at first sexual maturity of common pandora *Pagellus erythrinus* (Sparidae) from the Bay of Monastir (Tunisia, Central Mediterranean). Annales, Series Historia Naturalis, 24: 1-10.

Brawn, V.M. 1961. Reproductive behaviour of the cod (*Gadus callarias* L.). Behaviour, 18: 177-198.

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

De Vlaming, V., Grossman, G. & Chapman, F. 1982. On the use of the gonosomatic index. Comparative Biochemistry and Physiology - Part A: Physiology, 73: 31-39.

Druzhinin, A.D. 1974. Notes on the ecology of *Calamus brachysomus* (Pisces, Sparidae). Journal of Ichthyology, 16: 317-319.

Dubovitsky, A.A. 1977. Distribution, migration and some biological features of littlehead porgy (*Calamus proridens* Jordan and Gilbert, 1884) family Sparidae of the Gulf of Mexico. FAO Fisheries Report, 200: 23-143.

González, P. 2001. Biología reproductiva y conducta trófica de *Pinguipes chilensis* Valenciennes, 1833 (Perciformes, Pinguipedidae). Tesis de Magíster en Ciencias con mención en Zoología, Universidad de Concepción, Concepción.

González, P. & Oyarzún, C. 2003. Variabilidad de índices biológicos en *Pinguipes chilensis valenciennes* 1833 (Perciformes, Pinguipedidae): ¿están realmente correlacionados? Gayana, 66: 249-253.

Grau, A., Saborido-Rey, F., Pastor, E., Palmer, M., Massutí-Pascual, E., Quetglas, A., et al. 2016. Reproductive strategies of common dentex *Dentex dentex*: management implications. Mediterranean Marine Science, 17: 552-566.

Grier, H.J., Linton, J.R., Leatherland, J.F. & de Vlaming, V.L. 1980. Structural evidence for two different testicular types in teleost fishes. American Journal Anatomy, 159: 331-345.

Gwo, J.C. & Gwo, H.H. 1993 Spermatogenesis in the black porgy, *Acanthopagrus schlegeli* (Teleostei: Perciformes: Sparidae). Molecular Reproduction and Development, 36: 75-83.

Heyman, W.D., Grüss, A., Biggs, C.R., Kobara, S., Farmer, N.A., Karnauskas, M., et al. 2019. Cooperative monitoring, assessment, and management of fish spawning aggregations and associated fisheries in the US Gulf of Mexico. Marine Policy, 109: 1-54.

Horvath, M.L., Churchill, B.G. & Huntsman, G.R. 1990. Growth, mortality, reproduction and feeding of knobbed porgy, *Calamus nodosus*, along the southeastern United States coast. Bulletin of Marine Science, 46: 677-687.

Humason, G. 1979. Animal tissue techniques. W.H. Freeman & Co., New York.

Lambert, Y. & Dutil, J.D. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Science, 54: 104-112.

Leal-Espinoza, J.D. 2006. Distribución espaciotemporal de larvas de peces en Bahía Magdalena durante el desarrollo del evento El Niño (1997-1998). Tesis de Magíster en Ciencias, Centro Interdisciplinario de Ciencias Marinas, La Paz.

Le Cren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). Journal of Animal Ecology, 20: 201-219.

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

Lowerre-Barbieri, S.K., Tringali, M.D., Shea, C.P., Burnsed, S.W., Bickford, J., Murphy, M. & Porch, C.

2018. Assessing red drum spawning aggregations and abundance in the Eastern Gulf of Mexico: a multidisciplinary approach. ICES Journal of Marine Science, 76: 516-529.

Matus-Nivón, E., Ramírez-Sevilla, R., Martínez-Pecero, R. & Ortiz-Galindo, J.L. 1989. Descripción de la larva y juvenil del mojarrón *Calamus brachysomus* (Lockington) (Pisces: Sparidae). Investigaciones Marinas, CICIMAR, 4: 141-150.

Morgan, M.J. 2008. Integrating reproductive biology into scientific advice for fisheries management. Journal of Northwest Atlantic Fishery Science, 41: 37-51.

Mouine, N., Francour, P., Ktari, M. & Chakroun-Marzouk, N. 2007. The reproductive biology of *Diplodus sargus sargus* in the Gulf of Tunis (central Mediterranean). Scientia Marina, 71: 461-469.

Murua, H. & Saborido-Rey, F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. Journal of Northwest Atlantic Fishery Science, 33: 23-31.

Pankhurst, N.W. & Porter, M.J. 2003. Cold and dark or warm and light: variations on the theme of environmental control of reproduction. Fish Physiology and Biochemistry, 28: 385-389.

Pavlidis, M.A. & Mylonas, C.C. 2011. Sparidae: biology and aquaculture of gilthead sea bream and other species. Blackwell Publishing, West Sussex.

Saborido-Rey, F. 2004. Ecología de la reproducción y potencial reproductivo en las poblaciones de peces marinos. Curso de doctorado 2002-2004. Universidad de Vigo, Vigo.

Sadovy, Y. & Liu, M. 2008. Functional hermaphroditism in teleosts. Fish and Fisheries, 9: 1-43.

Sadovy, Y. & Shapiro, D.Y. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia, 1: 136-156.

Salas, S., Chuenpagdee, R., Charles, A. & Seijo, J.C. 2011. Coastal fisheries of Latin America and the Caribbean. FAO, Rome.

Sarre, G.A. & Potter, I.C. 1999. Comparisons between the reproductive biology of black bream *Acanthopagrus butcheri* (Teleostei: Sparidae) in four estuaries with widely differing characteristics. International Journal of Salt Lake, 8: 179-210.

Sheaves, M. 2006. Is the timing of spawning in sparid fishes a response to sea temperature regimes? Coral Reefs, 25: 655-669.

Sokal, R.R. & Rohlf, F.J. 2012. Biometry: the principles and practice of statistics in biological research. W.H. Freeman & Co., New York.

Tyler-Jedlund, A.J. 2009. Age, growth, and reproduction of *Calamus proridens*, the littlehead porgy, from the northeast Gulf of Mexico. Master's Theses of Science, University of South Florida Scholar Commons, Florida.

Tyler, C.R. & Sumpter, J.P. 1996. Oocyte growth and development in teleost. Reviews in Fish Biology and Fisheries, 6: 287-318.

Uribe, M.C., Grier, H.J. & Mejía-Roa, V. 2014. Comparative testicular structure and spermatogenesis in bony fishes. Spermatogenesis, 4: 1-13.

Waltz, W., Roumillat, A. & Wenner, C. 1982. Biology of the whitebone porgy, *Calamus leucosteus*, in the South Atlantic Bight. Fishery Bulletin, 80: 863-874.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. Australian Journal of Marine and Freshwater Research, 41: 199-222.