

Research Article

Biochemical composition and condition of wild blackfin snook *Centropomus medius* through the reproductive cycle

Minerva Maldonado-García¹ , Vicente Gracia-López¹ , Alexia Omont¹ 
Jesús Rodríguez-Romero¹ , Carlos Rosas-Vázquez²  & Manuel Carrillo³ 

¹Centro de Investigaciones Biológicas del Noroeste (CIBNOR), La Paz, BCS, México

²Universidad Nacional Autónoma de México, Campus SISAL, Sisal Yucatán, México

³Instituto de Acuicultura de Torre de la Sal (CSIC), Castelló, España

Corresponding author: Vicente Gracia-López (vinny@cibnor.mx)

ABSTRACT. The blackfin snook, *Centropomus medius*, is a valuable fish in American and Mexican markets, mainly from catches. Nonetheless, information and studies about the biology of this species still need to be made available; thus, its aquaculture should be developed. This study aimed to describe the seasonal changes of proximate composition during a reproductive cycle of *C. medius*, analyzing differences between tissues and their changes related to the reproductive process. The snook specimens were collected in Magdalena Bay, Baja California Sur, Mexico, and measured every month from September 2001 to November 2002. Liver, gonads, muscle tissue, and intraperitoneal fat (IPF) were sampled and weighed. The gonadosomatic index (GSI), hepatosomatic index (HSI), IPF ratio, and condition factor index (K) were calculated. The biochemical composition was analyzed in the gonad, liver, and muscle. The reproductive period (RP) of wild *C. medius* in Baja California Sur, Mexico, was from June to December. The spawning period was recorded at summer temperature (25-30°C) and photoperiod (>13 h daylight) starting in September. High GSI values (gonad development), low HSI values (lipid reserve mobilization), low IPF, and low K ratio were related to elevated temperatures. Moreover, variations were observed in protein, total lipid, triglycerides, and glycogen content in muscle, liver, and gonad according to the reproductive phase. A positive correlation was demonstrated between protein contents in muscle, gonad, and K, with lower concentrations during RP, while liver protein composition showed an opposite pattern. Lipids were mainly present in the liver, and the concentration decreased during RP while muscle increased. The results obtained in this study show differences in the proximate analyses in the liver, muscle, and gonads throughout the year concerning different phases of the reproductive cycle, indicating a great dependence of this process on the mobilization of reserves during *C. medius* reproduction. Therefore, understanding the feeding requirements to pursue the management of this species in captivity for aquaculture development is greatly important.

Keywords: *Centropomus medius*; fish reproduction; marine fish; proximate composition; reserve mobilization; broodstock

INTRODUCTION

Seafood consumption sustainability depends on aquaculture products since capture fisheries production stagnates and global demand grows rapidly (Guillen et al. 2019). Therefore, research on the reproductive bio-

logy of marine fish species with commercial value must consider those species as potential culture candidates. Mexico has developed various projects to study marine fish species with high commercial interest in recent years. Among these species, those that should be mentioned for the number of studies carried out and the

technological development achieved are: several species of snook, *Centropomus* sp. (Alvarez-Lajonchère & Tsuzuki 2008, Granados-Amores et al. 2020), snapper, *Lutjanus* sp. (Ibarra-Castro & Duncan 2007, Spanopoulos-Zarco et al. 2022), totoaba, *Totoaba macdonaldi* (González-Félix et al. 2021), puffer fish *Sphoeroides annulatus* (Martínez-Brown et al. 2019), almaco jack, *Seriola rivoliana* (Viader-Guerrero et al. 2021) and the leopard grouper, *Mycteroperca rosacea* (Maldonado et al. 2018).

The *Centropomus* sp. snooks are highly recognized fish for their quality with high commercial value and economic importance for the fisheries along the Atlantic and Pacific coasts of the American continent (Jimenez-Martinez et al. 2012). Currently, 12 species of snook that belong to the genus *Centropomus* (Rivas 1986) are captured by artisanal fisheries (Motta et al. 2016). Most of them are distributed in Mexico, where they are highly appreciated and have high market demand. Approximately 10,000 t of *Centropomus* are caught annually in Mexico, reaching the 10th place for its commercial value in the national market. The average annual production growth rate in the last decade was 3.28% (CONAPESCA 2020).

Studies on the biology and culture conditions of the snook are of great importance to increase knowledge and serve as the basis for helping management plans for developing this species' aquaculture. Snooks have been studied for many years (Tucker 1987, Peters et al. 1998, Gracia-Lopez et al. 2003, Maldonado-García et al. 2005, Alvarez-Lajonchère & Tsuzuki 2008, Yanes-Roca et al. 2009, Cerqueira & Tsuzuki 2009, Santos et al. 2009, Jimenez-Martinez et al. 2012, Concha-Frías et al. 2018, Abdo-de la Parra et al. 2020, Young et al. 2020, Arenas et al. 2021, Arriaga-Hernández et al. 2021, Costa e Silva et al. 2021). Various species have been held in captivity to determine their reproductive processes and spawning season to reach controlled reproduction and, subsequently, to obtain larvae and juveniles for growth such as *Centropomus undecimalis* (Ibarra-Castro & Duncan 2007, Young et al. 2020), *C. viridis* (Abdo-de la Parra et al. 2020, Arriaga-Hernández et al. 2021) and *C. parallelus* (Cerqueira & Tsuzuki 2009). Nonetheless, their cultivation continues to be in the early stages.

As a candidate species for cultivation on the Pacific coast, the blackfin snook, *Centropomus medius*, is a polycyclic species of high potential in aquaculture; few studies have been performed on this species, and its reproductive cycle has been determined from July to November for several years associated with higher seawater temperatures and longer daylight (Alvarez-

Lajonchère et al. 2001, Maldonado-García et al. 2005). Nonetheless, according to seasonal food consumption, broodfish store energy for somatic growth (accumulation of protein and lipids) or gonadal development (depletion of protein and lipids), following a seasonal pattern (Stickney & Torres 1989, Habib et al. 2021). Thanks to manipulating diet and environmental conditions, similar changes in cultured fish body composition can be elicited (Feltrin-Contente et al. 2009, Santos et al. 2009, Yanes-Roca et al. 2009).

Studies on body composition are important tools for evaluating cultured organisms' quality and physiological condition (Craig et al. 2000). According to the species, fecundity, egg size, and other parameters are influenced by the availability and quality of energetic reserves or by environmental conditions and food assimilation (Brooks et al. 1997). Moreover, throughout the spawning season, a considerable change has been observed in the proximate composition of tissues and energy dynamics associated with egg production of European hake *Merluccius merluccius* (Robin et al. 2003, Domínguez-Petit et al. 2010, Fuiman et al. 2013). In captive breeders, the reserve mobilization changes are also related to the annual reproductive fish cycle (Tolussi et al. 2018).

According to the literature, reserve mobilization could be addressed as follows: as ovarian growth rate increases, somatic growth also decreases. Meanwhile, lipids rapidly accumulate, reaching 41% dry matter values. Lipid content increases during ovary growth and fish oocyte volume; consequently, a decrease in the energetic value of dry matter is observed. These alterations in chemical composition mean that during vitellogenesis, the rate of lipid accumulation in ovaries is slower than protein accumulation (Dabrowski 1982, Newman et al. 2007); consequently, the energy content per ovary increases during this period. Changes in ovarian lipid content correspond to somatic body lipid content, of which the muscle is the main energy source for gonad formation (Dabrowski 1982). Additionally, the variation in energy in the muscles of different fish species has shown differences between the sexes and among the stages of gonad maturity, showing that the muscle energy variation indicates a function of the reproductive cycle (Espínola et al. 2014).

Furthermore, to ensure the sustainability of broodstock and continuity of the production in aquaculture, the fish condition is an important criterium to consider, which can be assessed using morphometric measures, such as length-weight relationship, condition factor (K), hepatosomatic (HIS) and gonadosomatic (GSI) indexes and biochemical measures as lipids,

proteins and other components (Domínguez-Petit et al. 2010). Moreover, the intraperitoneal fat (IPF) index can be linked to reproductive success and recruitment potential. Fish with higher IPF levels are more likely to produce viable offspring, contributing to better recruitment rates in the population (Pereira et al. 2018).

For *C. medius*, information about the relationship between the annual reproductive cycle, biochemical reserves, their mobilization, and fish condition is lacking. We can suppose that proximate composition in tissues and the condition index of *C. medius* would vary according to the reproductive cycle throughout the year. Thus, this research study aims to describe the seasonal changes of proximate composition during the reproductive cycle of the blackfin snook (*C. medius*), analyzing differences between tissues and their changes related to the reproductive process.

MATERIALS AND METHODS

Broodstock and tissue samples

The study was carried out under the Guidelines of the European Union Council (2010/63/EU) and the Mexican Government (NOM-062-ZOO-1999) for experimental animals' production, care, and use. Experimental protocols and procedures were reviewed and approved by the aquaculture committee at CIBNOR.

From September 2001 to November 2002, a total of 282 snook specimens (165 females and 117 males) were collected in a mangrove and estuarine area of Magdalena Bay, Baja California Sur, Mexico, using a 10 m long gill net with a 2 m high and 75 mm stretch mesh. Sampling was conducted monthly, where superficial temperature (°C) and salinity were measured in each sampling site, using a manual mercury thermometer and a Brix refractometer 0-90%. Natural photoperiod was calculated specifically for this zone (24°37'29"N and 111°58'24"W), following the methodology of Rodríguez et al. (2001). The specimens' total fish weight (TFW, g) and the standard length (SL, cm) were measured and dissected to sample liver, gonads, and muscle tissue below the first dorsal spine. The fat from the peritoneal cavity was isolated. Gonads, liver, and fat were weighed and recorded for each fish to calculate the GSI, HIS, and IPF ratio, expressed in percentage, as follows: $GSI = \text{total gonad weight} \times 100 / \text{TFW}$; $HIS = \text{liver weight} \times 100 / \text{TFW}$; and $IPF \text{ ratio} = \text{total fat weight} \times 100 / \text{TFW}$ (Craig et al. 2000). Finally, K for each fish was calculated: $K = \text{TFW} \times 100 / \text{SL}^3$.

Biochemical analyses

To proceed to the biochemical analyses, 0.1 ± 0.05 g gonadal, liver, and muscle samples were taken, weighed on an analytical balance, and placed in 1 mL Eppendorf (Eppendorf Corporate, Hamburg, Germany) tubes, which were stored at -80°C before being processed. The muscle, gonad, and liver samples were lyophilized and homogenized in 1 mL of cold physiological saline solution (0.9% NaCl 450 mM); 100 μL were taken from each sample for the different biochemical analyses.

Protein content was determined according to Bradford (1976), with absorbance measured at 595 nm and expressed in mg g^{-1} of tissue. A standard solution curve (bovine albumin), concentration 2 mg mL^{-1} , was performed with the following concentrations: 1.0, 0.5, 0.25, and 0.125 mg mL^{-1} . An isotopic solution (NaCl 450 mM) was used as a blank.

The Merck Diagnostic kit (Zöllner & Kirsch 1962) was used to determine total lipids; 0.1 mL of each tissue sample was taken and mixed with 1 mL of sulphuric acid. Then, they were stirred and heated in a 90°C water bath for 10 min and cooled in an ice bath. From each mixture obtained, 15 μL were taken and reacted with 200 μL of phosphoric acid-vanillin. The absorbance was measured at 560 nm, and lipid concentration was expressed in mg g^{-1} of tissue (Barnes & Blackstock 1973).

Triglyceride concentration was determined according to McGowan et al. (1983); 15 μL of gonadal, liver, and muscle samples were taken, and 200 μL of GPO-Trinder reagent was added. The absorbance was measured at 540 nm at room temperature for 20 min, and triglycerides were quantified as triglyceride units using a Sigma CARDIOLIPID™ (Sigma-Aldrich, St. Louis, MO, USA) solution as a standard and expressed in mg g^{-1} of tissue. The triglyceride unit corresponds to the quantity of 4-(p-benzoquinone imine) phenazone per minute, resulting from triglyceride oxidation.

Glycogen concentration was determined according to the Anthrone method (Van Handel 1965); 15 μL of gonadal, liver, and muscle samples were homogenized in 5 mL of cold 10% trichloroacetic acid and centrifuged at 3000 rpm at -5°C for 15 min; then, 1 mL of the supernatant was mixed with 5 mL of 95% ethanol and centrifuged under the same conditions. The supernatant was discarded, and the glycogen pellet was resuspended in 0.5 mL distilled water; 4 mL of Anthrone reagent (0.1% dissolved in 76% sulfuric acid) were added to tubes, which were incubated at 90°C for 10 min and then cooled at 4°C to stop further reaction.

Absorbance was measured in a spectrophotometer at 620 nm against a reagent blank, and glycogen was quantified as glycosyl units using glucose solution as a standard and expressed in mg g^{-1} of tissue.

Total cholesterol was determined in gonad samples using the CHOD-PAP method (Allain et al. 1974). Briefly, 1 mL of prepared reactant containing cholesterol esterase (CE), cholesterol oxidase (CHOD), peroxidase (POD), and 4-aminoantipyrine (4-AAP) in buffer was added to 10 μL of the sample to form a quinonimine dye. The reaction lasted 15 min at room temperature; then, absorbance was measured in a spectrophotometer at 492 nm. Total cholesterol concentration was expressed in mg g^{-1} of tissue.

Statistical analyses

Arcsine transformation was applied to the GS and HSI before the statistical analyses to verify normality, tested by Kolmogorov-Smirnov analysis. The analysis of variance (ANOVA) was determined by the general linear model (GLM) multiple dependent variables (MANOVA). Monthly homogeneity was estimated by Tukey's honestly significant difference (HSD) test with significance at $P < 0.05$. The data obtained were processed using the software Statistica for Windows 5.5 (Tulsa, OK, USA).

RESULTS

Photoperiod and temperature

Water temperature was higher in September and October, reaching $27 \pm 0.3^\circ\text{C}$. Then, a constant decrease was recorded until April, May, and June with temperatures of $16 \pm 0.5^\circ\text{C}$ (Fig. 1). The photoperiod measured as daylight showed a maximum of 14 h during summer and 11 h in winter.

Length and weight

The SL for females ranged from 35.6 to 49.2 cm and for males from 27.4 to 40.4 cm, with a mean and standard error (SE) of 40.7 ± 4.0 and 35.8 ± 4.1 cm, respectively (Table 1). The TFW of females ranged from 325 to 850 g and 236 to 637 g for males, with a mean and SE of 605 ± 183 and 425 ± 132 g, respectively (Table 1). Finally, K ranged from 0.72 to 1.13 for females and 0.73 to 1.17 for males, with a mean and SE of 0.84 ± 0.11 and 0.87 ± 0.12 , respectively.

Biological index (GSI, HSI, IPF)

In 2001 and 2002, GSI for females varied from 0.31 to 0.98%, showing significant differences between months ($P < 0.05$) with a period of minimum average

values from December (post-spawning period) (0.41%) to May (0.31%), which correspond to the pre-gametogenesis period. An increase in the GSI average values was observed from July to November (up to 0.86%), where a large number of mature individuals were observed in the sample (Fig. 2a). For males, the average GSI values showed a similar pattern as in females, where the lowest values were observed from December to May, which correspond to the period from the end of the spawning season to the end of pre-gametogenesis. The GSI average values ranged from 0.31 to 0.58%.

Furthermore, HSI also showed significant monthly variations ($P < 0.05$). In females, the average index values were the lowest in August-November (0.61 to 0.63%), which corresponds to the spawning period (Fig. 2b). The highest average values were found during the post-spawning period in December (0.95%) and during the pre-gametogenesis period from January to July (0.87 to 0.81%). The results observed in males showed a similar trend as females with a high HSI index during the pre-gametogenesis period from December to August (0.73 to 0.93%) and lower values during the reproductive period (RP) in October and November (0.53 to 0.60) ($P < 0.05$).

The IPF ratio observed for females and males followed a similar pattern to the HSI index, with significant differences among months ($P < 0.05$) (Fig. 3). For males, the results were higher from January to March, but declined significantly to reach low values from April to December. Significant differences ($P < 0.05$) were obtained between these two groups of months correlated with the reproductive and spawning period, respectively. Moreover, the IPF ratio for females increased during the pre-gametogenesis period from December to February. The lowest values were observed during the RP from May to December (Fig. 3).

Biochemical analyses

Muscle

Protein concentration in the muscles of males and females was variable throughout the annual cycle (Fig. 4a) with significant monthly variations ($P < 0.05$). In both sexes, higher values were recorded during the first four months of the resting phase, with the highest value observed in January for females ($425.07 \pm 23.14 \text{ mg g}^{-1}$). The protein content in muscle was maintained below 250 mg g^{-1} two months before and during the RP. Lower protein content was detected in May for both sexes: 77.03 ± 25.44 and $75.24 \pm 18.75 \text{ mg g}^{-1}$ for males and females, respectively.

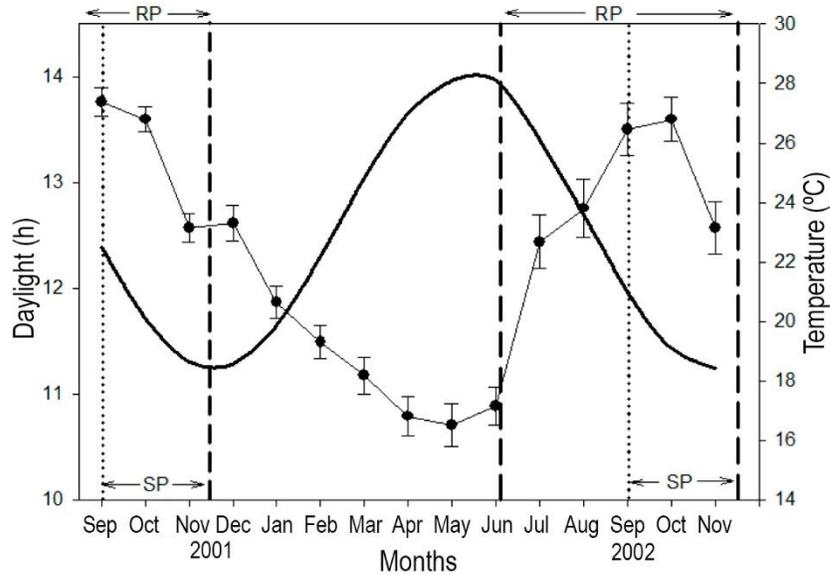


Figure 1. Photoperiod (continuous-line) and temperature (spotted-line) during two sexual cycles of the blackfin snook *Centropomus medius*. Values are given as means \pm standard error. RP: reproduction period; SP: spawning period.

Table 1. Monthly variability of weight, length, and condition factor (K) of *Centropomus medius* female and male during two sexual cycles.

Month	Female			Male		
	Weight (g)	Length (cm)	K	Weight (g)	Length (cm)	K
Sep 2001	457 \pm 62	37.0 \pm 1.2	0.90 \pm 0.06	349 \pm 89	35.5 \pm 5.5	0.80 \pm 0.16
Oct	472 \pm 34	38.9 \pm 0.9	0.80 \pm 0.08	381 \pm 82	35.3 \pm 2.9	0.85 \pm 0.06
Nov	325 \pm 49	35.6 \pm 0.2	0.72 \pm 0.10	327 \pm 27	33.9 \pm 1.2	0.84 \pm 0.06
Dec	450 \pm 53	39.2 \pm 2.5	0.75 \pm 0.07	386 \pm 76	36.3 \pm 1.6	0.80 \pm 0.08
Jan 2002	829 \pm 278	41.5 \pm 4.5	1.13 \pm 0.08	637 \pm 137	37.9 \pm 3.7	1.17 \pm 0.10
Feb	524 \pm 90	38.8 \pm 3.2	0.93 \pm 0.32	563 \pm 136	40.0 \pm 3.0	0.87 \pm 0.06
Mar	652 \pm 143	42.4 \pm 3.1	0.85 \pm 0.06	556 \pm 128	40.4 \pm 2.4	0.83 \pm 0.09
Apr	528 \pm 47	40.6 \pm 2.0	0.79 \pm 0.06	440 \pm 72	37.3 \pm 3.1	0.87 \pm 0.32
May	818 \pm 197	46.0 \pm 3.1	0.84 \pm 0.07	300 \pm 53	30.4 \pm 3.0	1.11 \pm 0.07
Jun	-	-	-	-	-	-
Jul	850 \pm 197	49.2 \pm 5.1	0.72 \pm 0.06	577 \pm 89	40.1 \pm 3.8	0.73 \pm 0.08
Aug	750 \pm 126	38.5 \pm 5.6	0.82 \pm 0.11	511 \pm 76	39.3 \pm 2.0	0.83 \pm 0.10
Sep	-	-	-	-	-	-
Oct	-	-	-	236 \pm 96	31.2 \pm 4.8	0.79 \pm 0.07
Nov	-	-	-	257 \pm 56	27.4 \pm 2.8	0.86 \pm 0.09

Lipid concentration in muscle (Fig. 4b) showed a similar trend as protein content. The highest values were recorded during the resting phase, with $10.41 \pm 0.84 \text{ mg g}^{-1}$ in February for males, and $8.19 \pm 1.07 \text{ mg g}^{-1}$ in March for females. The lowest values ($P < 0.05$) were recorded at the end of the RP of 2001, with $2.73 \pm 0.52 \text{ mg g}^{-1}$ in November for males, and $2.53 \pm 0.78 \text{ mg g}^{-1}$ in October for females. Nonetheless, during the 2002 spawning period, the muscles of males showed newly high concentrations of lipids compared to the rest of the year.

Regarding triglyceride content in muscle (Fig. 4c), males and females showed a significantly different pattern ($P < 0.05$). Males and females had the highest muscle triglyceride concentration at the end of the RP (respectively 4.43 ± 0.71 and $4.56 \pm 0.44 \text{ mg g}^{-1}$); moreover, females showed an increase in triglyceride content at the beginning of RP ($4.12 \pm 0.53 \text{ mg g}^{-1}$). For the rest of the year, the triglyceride content in the muscles of both sexes remained relatively constant, with values that ranged from 1.21 to 3.17 mg g^{-1} .

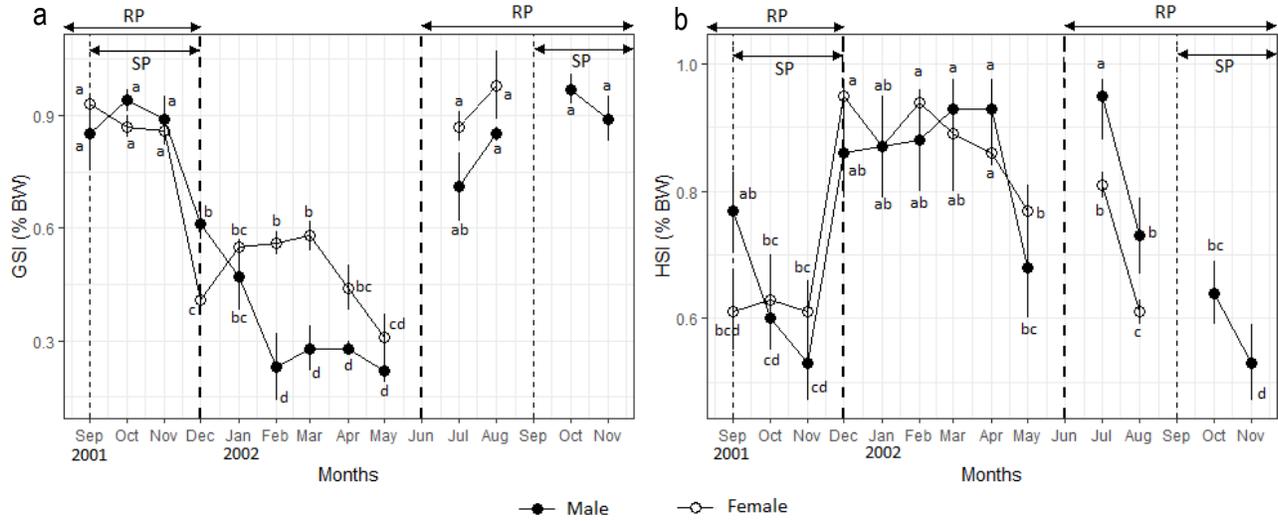


Figure 2. Monthly variability of a) gonadosomatic index (GSI) (% of body weight, BW) and b) hepatosomatic index (HSI) (% of BW) of female and male of *Centropomus medius* during two sexual cycles. Different letters indicate significant ($P < 0.05$) differences between months and sex (mean \pm standard error). RP: reproductive period; SP: spawning period.

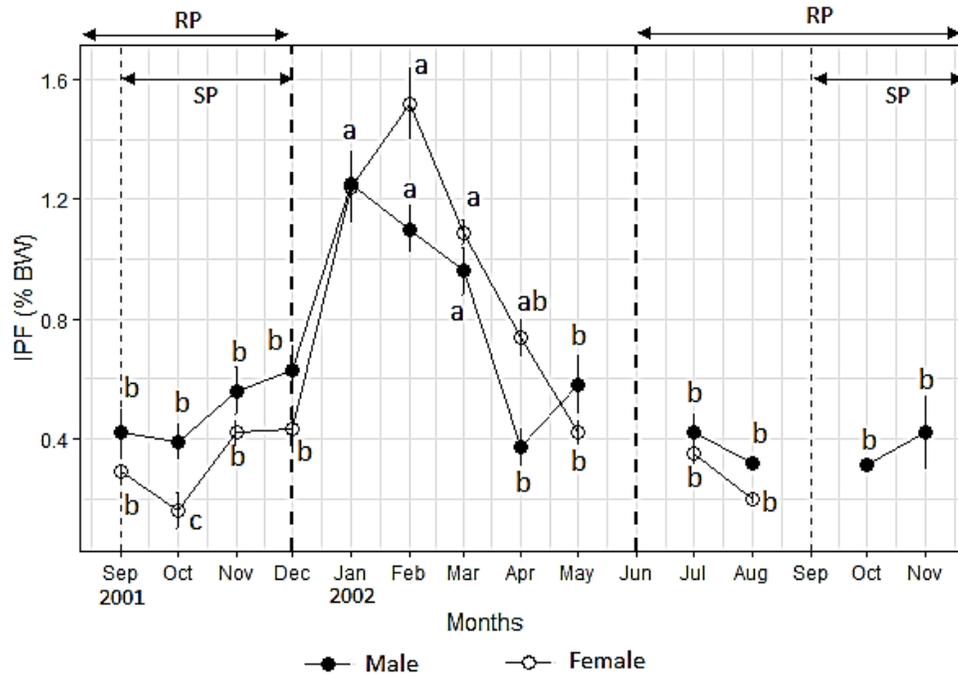


Figure 3. Monthly variability of *Centropomus medius* intraperitoneal fat (IPF) ratio (% of body weight, BW) during two sexual cycles. Different letters indicate significant ($P < 0.05$) differences between months and sex (mean \pm standard error). RP: reproductive period; SP: spawning period.

Finally, glycogen concentration (Fig. 4d) also showed a similar trend as protein and lipid contents, with higher values during the first months of the resting period. In males, muscle glycogen content was higher in January ($1.08 \pm 0.07 \text{ mg g}^{-1}$) and in females in

February ($1.11 \pm 0.15 \text{ mg g}^{-1}$). Significant lower concentrations were observed during the 2022 reproductive period, with values below 0.50 mg g^{-1} in both males and females.

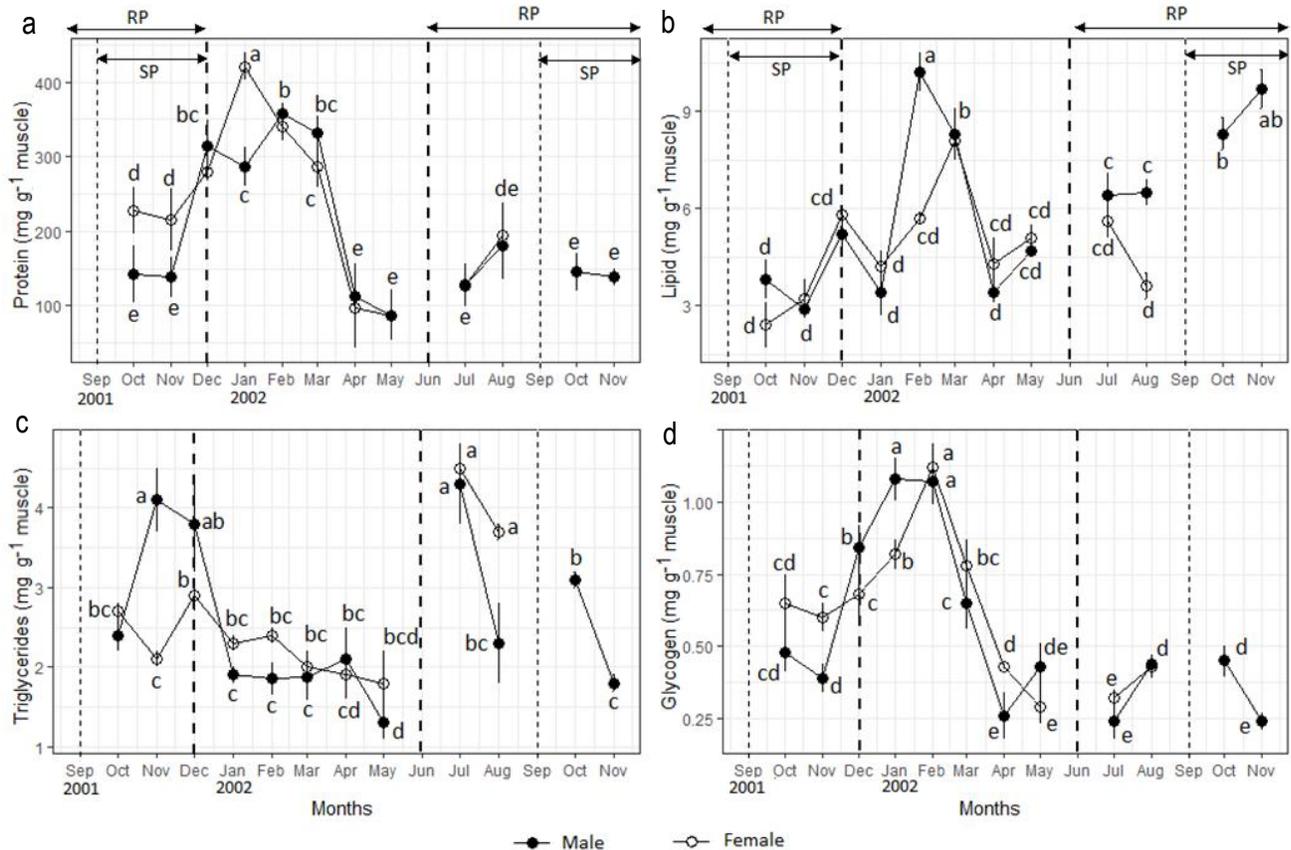


Figure 4. Monthly variability of a) protein, b) lipid, c) triglyceride, and d) glycogen concentrations in muscles of *Centropomus medius* female and male during two sexual cycles. Different letters indicate significant ($P < 0.05$) differences between months and sex (mean \pm standard error). RP: reproductive period; SP: spawning period.

Gonads

Protein content in gonads (Fig. 5a) followed the same pattern for males and females. The lowest values were recorded during the reproduction period (40.16 ± 8.97 mg g⁻¹ in August for males, and 70.80 ± 4.21 mg g⁻¹ in October for females); the highest gonad protein contents were during the last month of the reproductive phase for females (November; 145.90 ± 11.42 mg g⁻¹) and during the resting period for males (March; 148.65 ± 9.68 mg g⁻¹).

On the contrary, lipid, cholesterol, and triglyceride concentrations in gonads showed a trend where the highest values were found during the reproductive and spawning periods. Lipid content (Fig. 5b) in male gonads was still homogeneous all year long with few variations from 1.54 ± 0.67 to 2.87 ± 0.46 mg g⁻¹. Female gonads showed a significant increase in lipid content in August (5.75 ± 0.26 mg g⁻¹). Triglyceride concentration in gonads (Fig. 5c) showed no significant difference between males and females. The lowest values were recorded in January (0.41 ± 0.11 and 0.42

± 0.08 mg g⁻¹, respectively) and increased during the resting phase to reach in August the highest concentration (1.34 ± 0.05 and 1.43 ± 0.09 mg g⁻¹, respectively). Finally, the glycogen content in gonads (Fig. 5d) of both sexes was lower than the detection value of the kit (0.05 mg g⁻¹) during the resting phase. It increased until reaching its maximum during October and November with 3.11 ± 0.41 mg g⁻¹ in females, and 4.45 ± 0.47 mg g⁻¹ in males, respectively.

Liver

Liver protein (Fig. 6a) showed a seasonal pattern for both sexes during the annual cycle with significant differences between months ($P < 0.05$). Liver protein concentrations in males and females were lower during the resting phase, principally with the lowest values from December to March (99.21 ± 15.10 and 116.66 ± 12.81 mg g⁻¹, respectively). The highest values were recorded during the reproductive phase, particularly in September: 184.99 ± 4.01 mg g⁻¹ for males and 188.79 ± 15.47 mg g⁻¹ for females.

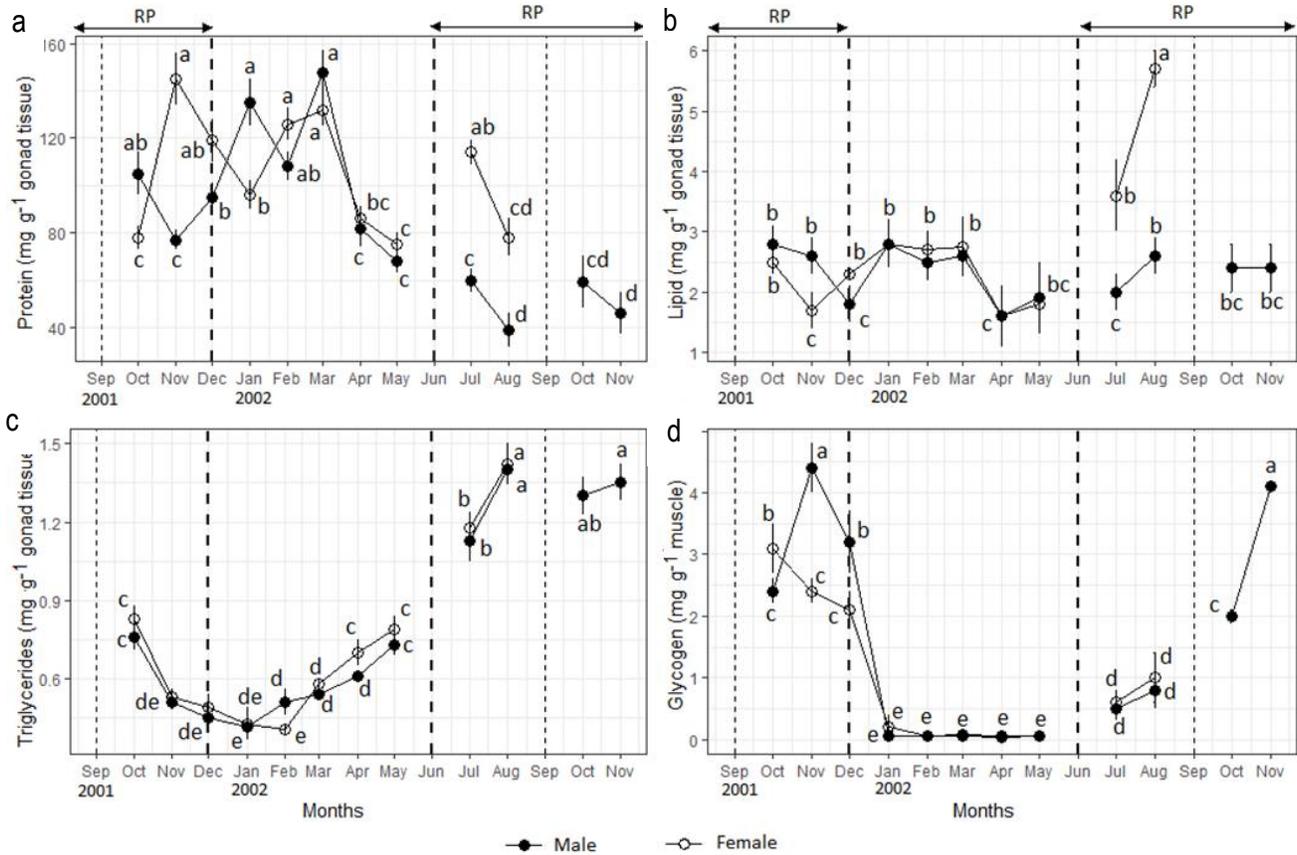


Figure 5. Monthly variability of a) protein, b) lipid, c) triglyceride, and d) glycogen concentrations in *Centropomus medius* female and male gonads during two sexual cycles. Different letters indicate significant ($P < 0.05$) differences between months and sex (mean \pm standard error). RP: reproductive period; SP: spawning period.

Lipid and triglyceride contents in the liver (Figs. 6b-c) showed a remarkable seasonal pattern in both sexes. The reproductive period started with high concentrations of both elements in the liver (lipids: 42.80 ± 0.75 and 49.32 ± 3.76 mg g^{-1} ; triglycerides: 1.1 ± 0.1 and 1.2 ± 0.1 mg g^{-1} for males and females, without significant difference between sexes in this last case).

DISCUSSION

Photoperiod and water temperature are two of the most relevant factors influencing reproductive cycles and timing of spawning in *Centropomus* sp. (Cerqueira & Tsuzuki 2009, Perera-García et al. 2010, Herkenhoff et al. 2023). The photoperiod is related to both previtellogenesis and vitellogenesis periods under the control of an endogenous biological rhythm in teleost fishes (Bon et al. 1997, Nyuji et al. 2018, García-Vega et al. 2022, Yeldham et al. 2023). The individuals used in this study were captured in a shallow-water coastal mangrove area in the western part of the Baja California

Peninsula. This area has a marked thermal difference between the months of reproductive rest (January-June), where the temperature decreases from 20 to 17°C and is lower than the months where gametogenesis and spawning are observed (June-December), with temperatures higher than 22°C. On the contrary, since the common snook, *C. undecimalis* is located in warmer waters, the spawning season is longer (April to January) and includes multiple spawning, most of them occurring from May to September, and especially during new and full moons (Peters et al. 1998). Independently of the location, the spawning period of the snook was recorded at temperatures from 25 to 30°C (Cerqueira & Tsuzuki 2009, Herkenhoff et al. 2023) and when the photoperiod exceeds 13 h of daylight (Peters et al. 1998). Thus, the results in this study lead to the same conclusion for *C. medius*.

The correlation between water temperature, photoperiod, and the stage of gonadal development has been demonstrated previously (Maldonado-García et al. 2005), revealing the correlation between high GSI

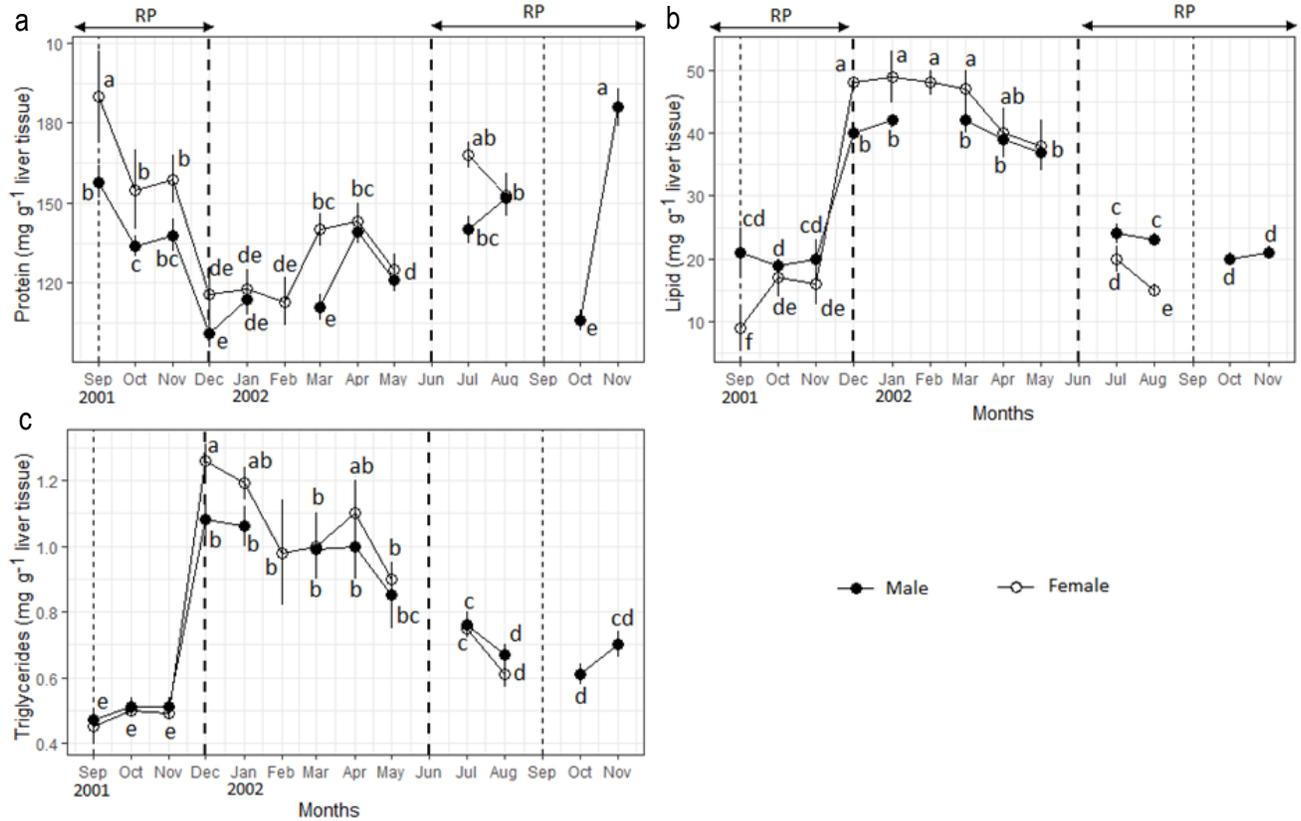


Figure 6. Monthly variability of a) protein, b) lipid, and c) triglyceride concentrations in the liver of *Centropomus medius* females and males during two sexual cycles. Different letters indicate significant ($P < 0.05$) differences between months and sex (mean \pm standard error). RP: reproductive period; SP: spawning period.

values (gonad development), low HSI values (lipid reserve mobilization) and elevated temperatures. This study continued with the seasonality correlation by demonstrating that the IPF ratio is also negatively related to temperature and photoperiod with the maximum recorded and the beginning of the resting period (December to March). The increase of IPF is also related to the accumulation of reserves by fish during the resting period. The correlation of IPF, GSI, and HSI in fish from temperate water areas depends principally on the seasonal food availability (Taylor et al. 2000, Perera-García et al. 2010, Young et al. 2020). Stickney & Torres (1989) demonstrated that energy reserves are less essential for fish living in stable climates since food is relatively durable all year. Therefore, since *C. medius* of this study comes from a tropical environment, its resting period corresponds to winter when water productivity is higher, and it can accumulate reserves related to growth (Stickney & Torres 1989). As observed in this study, the weight and size of the specimens collected during January 2002 were bigger than the rest of the year, with a condition

factor (K) closer to 1. During summer, the reserves are mobilized for reproduction, which is reflected in sizes, and K. Atsé et al. (2009) revealed that in *Tylochromis jentinki*, the increasing HSI and K corresponded to oocyte growth; spawning led to a decrease of these two variables because fish slowed their feeding behavior during this period and started using hepatic reserves to ensure their energetic needs (Young et al. 2020). This reproduction strategy seems to be the same in this study's case of *C. medius*.

The GSI, HSI, and IPF are good indexes to measure the energy reserves of fish (Shulman & Love 1999). Still, the proximate composition of tissues describes more precisely the fish condition and allows an understanding of energy mobilization (Domínguez-Petit et al. 2010, Young et al. 2020). Body composition of *Centropomus* sp. changes in response to environmental conditions and seasons (Feltrin-Contente et al. 2009, Santos et al. 2009, Yanes-Roca et al. 2009, Perera-García et al. 2010, Young et al. 2020). This study revealed that in *C. medius*, there were variations of protein, total lipid, triglycerides, and

glycogen content in muscle, liver, and gonad according to the season. Protein contents showed a similar pattern but at different periods depending on the tissue: values were two times higher in the liver from September to November, in the muscle from December to March, and in the gonad from October to March, compared to the rest of the year. One of the reasons for protein variation in muscle during the year - independently of sex - is food availability (Habib et al. 2021). Thus, food availability is better during winter because of the optimal water temperature for developing zooplankton and phytoplankton at the localization site of this study (Chang et al. 2014). Differences in protein content between sexes have been observed in the gonad before the spawning phase and in the liver and muscle during the spawning phase: protein contents in female organs were significantly higher than in males. Medda et al. (1980) demonstrated that in *Heteropneustes fossilis* vitellogenic females, estrogen increased protein content in the liver. Since estrogen is the principal hormone responsible for oocyte growth within the gonads (Nagahama et al. 1995), the synthesis of estrogen before the reproductive period in female *C. medius* led to increasing protein mobilization in the gonad during gametogenesis (higher GSI) and in the liver during the spawning phase. During gonad maturation, protein mainly stored in muscle seems to be transferred to the gonad, as observed in the results obtained in this study. These findings were similar to those reported by Tolussi et al. (2018), who concluded that the main source of protein transferred to the ovaries at the vitellogenic stage came from muscle and is positively correlated with GSI. Moreover, a positive correlation between protein contents in muscle and gonad and K was observed. The same correlation has been observed previously in *Coregonus lavaretus*, concluding that healthy fish (K close to 1) are likely to be more successful in breeding (Dörücü 2000).

Muscle glycogen has almost the same monthly variation pattern as protein, suggesting the mobilization of reserves to gonad maturation. This study demonstrated the increase of muscle protein and glycogen during previtellogenesis and decreased during spawning. These nutrients were mobilized to somatic growth as observed for the freshwater catfish, *Tandanus tandanus*, which may be associated with higher protein synthesis requirements of females for preparation of reproductive activities (Tripathi & Verma 2004).

At the beginning of vitellogenesis, proteins and lipids stored mainly in fish liver and muscle are transported to the gonads to contribute to the egg

reserves or energy substrate for lipoprotein synthesis (Almansa et al. 2001). According to this observation, the results in this study revealed that lipid content increased only in female gonads during the vitellogenesis period and decreased in muscle and liver after the resting period. However, for males, even if the lipid content in muscle and liver showed the same variations as females, no change in lipid content has been observed in male gonads. Sardenne et al. (2022) also observed that lipid concentrations remained unchanged during the reproductive cycle of the male Mediterranean swordfish *Xiphias gladius*. Moreover, Maldonado-García et al. (2005) reported that males of blackfin snook have sperm in May and are potentially reproductive two months longer than females. In marine fishes such as the angelfish *Holocanthus passer*, males mature one month earlier than females (Arellano-Martínez et al. 1999). These authors suggested that due to the smaller size of the male gonad compared to females, males probably require less energy for gonad development and may start to mature earlier than females. These results lead to the conclusion that the lipid reserves of males during the reproduction period are not destined for gonad reserves but might be used for energy needs during the courtship process or hormonal production.

The hepatic triglycerides increased during the resting phase and reached a minimum during spawning for both *C. medius* males and females, while gonad triglycerides showed an opposite trend. The same observations have been made for the catfish *Heteropneustes fossilis* (Singh & Singh 1990), suggesting that during reproduction, the calorific demand for spawning behavior combines with the reduced food intake and activates the lipolysis of triglycerides for plasma transfer to the gonad or as an intermediate source of energy. The same observation has been made for yellowfin tuna, where total muscle lipid content was low and constant throughout ovarian development, and liver total lipid content was the main fuel for the reproduction process (Zudaire et al. 2014). On the contrary, *Katsuwonus pelamis* supports reproduction directly from food intake over the breeding season: GHI and HSI were positively correlated with lipid content in gonads and liver, and fat content in the main storage tissues was consumed as the ovary developed (Grande et al. 2016).

As the blackfin snook, carnivorous fish get metabolically functional energy for reproduction from intraperitoneal fat and liver lipid reserves, such as triglycerides. Changes in lipid concentrations, especially in fatty acid composition, and in tissues during

the reproductive cycle have been observed for different species, for example, seabreams (Almansa et al. 2001, Cejas et al. 2004a,b), amberjack (Rodríguez-Barreto et al. 2012), stinger (Li et al. 2018) and totoaba (González-Félix et al. 2021). Li et al. (2018) demonstrated that the fatty acids composition of the broodstock was tissue- and lipid class-specific. During sexual maturation, polar lipid content significantly decreases in the ovary, but neutral lipid content significantly increases. In the stinger gonad, high-unsaturated fatty acids, such as arachidonic, docosahexaenoic, and eicosapentaenoic acids, are selectively transferred and conserved, indicating the crucial role of these fatty acids during sexual maturation of this fish species. Since the results of the different classes of lipids in the various tissues may be different during the reproductive cycle, future studies on the blackfin snook may help to know the maturation of each individual in the reproductive phases.

Finally, other related studies have shown that the control of the factors that affect nutrient mobilization for developing embryos, as well as the criteria for assessing the quality of the eggs produced and broodstock fitness, are of paramount importance for the reproductive success of any particular species which are relevant for aquaculture. These factors can act as determinants of the quality of the progeny, as well as indicators of both the quality of the eggs and broodfish physiology (Carrillo et al. 2000). The results in this study give us insight into the photoperiod and temperature conditions required for this species; information that will help to earlier or delay the spawning period of the broodstock that are kept in captivity. Modifying these aquaculture conditions will allow us to forecast or control egg production throughout the year and consequently achieve a productive juvenile culture, a goal for the aquaculture production sector. Knowing the amount or the profile of proteins, lipids, and triglycerides that the snook *C. medius* has during its resting and reproductive period helps estimate the physiological nutritional condition this species requires in captivity. Therefore, our data serves as a reference to acknowledge the dietary needs that are desirable to improve the broodstock quality and to prepare them for the spawning season, which can be translated to better egg quality and, consequently, a healthier stock of juveniles. Research studies related to the basic reproductive biology of commercial marine fish offer data to a productive sector that gives the understanding to determine the best conditions in captivity and how to improve both reproductive and nutritional conditions.

ACKNOWLEDGMENTS

This research study was funded by CONACyT (Consejo Nacional de Ciencia y Tecnología) Mexico (Project SEP-CONACyT 2001-2003 35162B, PRONACE CONAHCYT 321279). The authors acknowledge Diana Carreño, Roberto Hernández, and Marcela Linares for their help in the sample analyses and Antonio Luna and Diana Fischer for the English edition and to CONACyT for the national scholarship N°894930.

REFERENCES

- Abdo-de la Parra, M.I., Rodríguez-Ibarra, L.E., Ibarra-Castro, L., Martínez-Brown, J.M. & Velasco-Blanco, G. 2020. Effects of frequency and feeding time on growth, food utilization, somatic indexes and survival of juvenile white snook *Centropomus viridis*. *Ciencias del Mar*, 46: 155-163. doi: 10.7773/cm.v46i3.3089
- Allain, C.C., Poon, L.S., Chan, C.S.G., Richmond, W. & Fu, P.C. 1974. Enzymatic determination of total serum cholesterol. *Clinical Chemistry*, 20: 470-475. doi: 10.1093/clinchem/20.4.470
- Almansa, E., Martian, M., Cejas, J.R., Badi, P., Jerez, S. & Lorenzo, A. 2001. Lipid and fatty acid composition of female gilthead seabream during their reproductive cycle: effects of a diet lacking n-3 HUFA. *Journal of Fish Biology*, 59: 267-286. doi: 10.1111/j.1095-8649.2001.tb00129.x
- Alvarez-Lajonchère, L. & Tsuzuki, M.Y. 2008. A review of methods for *Centropomus* spp. (snooks) aquaculture and recommendations for the establishment of their culture in Latin American. *Aquaculture Research*, 39: 684-700. doi: 10.1111/j.1365-2109.2008.01921.x
- Alvarez-Lajonchère, L., Guerrero-Tortolero, D. & Perez-Urbiola, J.C. 2001. Validation of an ovarian biopsy method in a sea bass, *Centropomus medius* Günther. *Aquaculture Research*, 32: 379-384. doi: 10.1046/j.1365-2109.2001.00570.x
- Arellano-Martínez, M., Ceballos-Vázquez, B.P., García-Domínguez, F. & Galván-Magaña, F. 1999. Reproductive biology of the king angelfish *Holocanthus passer* Valenciennes 1846 in the Gulf of California, Mexico. *Bulletin of Marine Science*, 65: 677-689.
- Arenas, M., Álvarez-González, C.A., Barreto, A., Sánchez-Zamora, A., Suárez-Bautista, J., Cuzon, G., et al. 2021. Physiological and metabolic protein-sparing effects of dietary lipids on common snook *Centropomus undecimalis* (Bloch, 1792) juveniles.

- Aquaculture Nutrition, 27: 1089-1102. doi: 10.1111/anu.13250
- Arriaga-Hernández, D., Hernández, C., Martínez-Montaño, E., Ibarra-Castro, L., Lizárraga-Velázquez, E., Leyva-López, N., et al. 2021. Fish meal replacement by soybean products in aquaculture feeds for white snook, *Centropomus viridis*: effect on growth, diet digestibility, and digestive capacity. Aquaculture, 530: 735823. doi: 10.1016/j.aquaculture.2020.735823
- Atsé, B.C., Konan, K.J. & Kouassi, N.J. 2009. Biologie de la reproduction du Cichlidae *Tylochromis jentinki* dans la lagune Ebrié (Côte d'Ivoire). Cybium, 33: 11-19.
- Barnes, H. & Blackstock, J. 1973. Estimation of lipids in marine animals and tissues: detailed investigation of the sulphophosphovanilun method for 'total' lipids. Journal of Experimental Marine Biology and Ecology, 12: 103-118. doi: 10.1016/0022-0981(73)90040-3
- Bon, E., Corraze, G., Kaushik, S. & Le Menn, F. 1997. Effects of accelerated photoperiod regimes on the reproductive cycle of the female rainbow trout: I. Seasonal variations of plasma lipids correlated with vitellogenesis. Comparative Biochemistry and Physiology - Part A: Physiology, 118: 183-190. doi: 10.1016/S0300-9629(96)00415-X
- Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Analytical Biochemistry, 72: 248-254. doi: 10.1016/0003-2697(76)90527-3
- Brooks, S., Tyler, C.R. & Sumpter, J.P. 1997. Egg quality in fish: what makes a good egg? Reviews in Fish Biology and Fisheries, 7: 387-416. doi: 10.1023/A:1018400130692
- Carrillo, M., Zanuy, S., Oyen, F., Cerdá, J., Navas, J.M. & Ramos, J. 2000. Some criteria of the quality of the progeny as indicators of physiological broodstock fitness. Recent advances in Mediterranean aquaculture finfish species diversification. CIHEAM, Zaragoza, pp. 61-73.
- Cejas, J.R., Almansa, E., Jérez, S., Bolaños, A., Felipe, B. & Lorenzo, A. 2004a. Changes in lipid class and fatty acid composition during development in white seabream (*Diplodus sargus*) eggs and larvae. Comparative Biochemistry and Physiology - Part B: Biochemistry & Molecular Biology, 139: 209-216. doi: 10.1016/j.cbpc.2004.07.010
- Cejas, J.R., Almansa, E., Jérez, S., Bolaños, A., Samper, M. & Lorenzo, A. 2004b. Lipid and fatty acid composition of muscle and liver from wild and captive mature female broodstocks of white seabream, *Diplodus sargus*. Comparative Biochemistry and Physiology - Part B: Biochemistry & Molecular Biology, 138: 91-102. doi: 10.1016/j.cbpc.2004.03.003
- Cerqueira, V.R. & Tsuzuki, M.Y. 2009. A review of spawning induction, larviculture, and juvenile rearing of the fat snook, *Centropomus parallelus*. Fish Physiology and Biochemistry, 35: 17-28. doi: 10.1007/s10695-008-9245-y
- Chang, C.W., Shiah, F.K., Wu, J.T., Miki, T. & Hsieh, C.H. 2014. The role of food availability and phytoplankton community dynamics in the seasonal succession of zooplankton community in a subtropical reservoir. Limnologia, 46: 131-138. doi: 10.1016/j.limno.2014.01.002
- Comisión Nacional de Acuicultura y Pesca México (CONAPESCA). 2020. Anuario estadístico de acuicultura y pesca 2020. CONAPESCA, Mazatlán.
- Concha-Frías, B., Alvarez-González, C.A., Gaxiola, G., Chiappa, X., Sánchez-Zamora, A., Martínez-García, R., et al. 2018. Dietary protein requirement in common snook (*Centropomus undecimalis*) juveniles reared in marine and brackish water. Ecosistemas y Recursos Agropecuarios, 5: 45-54. doi: 10.19136/era.a5n13.1393
- Costa e Silva, G.H., Freitas, M.O. & Abilhoa, V. 2021. Reproductive biology of the fat snook *Centropomus parallelus* Poey, 1860 (Teleostei, Centropomidae) and implications for its management in the southern Atlantic Ocean. Journal of Fish Biology, 99: 669-672. doi: 10.1111/jfb.14718
- Craig, S.R., MacKenzie, D.S., Jones, G. & Gatlin, D.M. 2000. Seasonal changes in the reproductive condition and body composition of free-ranging red drum, *Sciaenops ocellatus*. Aquaculture, 190: 89-102. doi: 10.1016/S0044-8486(00)00386-0
- Dabrowski, K.R. 1982. Seasonal changes in the chemical composition of fish body and nutritional value of the muscle of the pollan (*Coregonus pollan* Thompson) from Lough Neagh, Northern Ireland. Hydrobiologia, 87: 121-141.
- Domínguez-Petit, R., Saborido-Rey, F. & Medina, I. 2010. Changes of proximate composition, energy storage, and condition of European hake (*Merluccius merluccius*, L. 1758) through the spawning season. Fish Research, 104: 73-82. doi: 10.1016/j.fishres.2009.05.016
- Dörücü, M. 2000. Changes in the protein and lipid content of muscle, liver and ovaries in relation to *Diphyllobothrium* spp. (Cestoda) infection in Powan (*Coregonus lavaretus*) from Loch Lomond, Scotland. Turkish Journal of Zoology, 24: 211-218.

- Espínola, L.A., Amsler, M.L., Paira, A.R., Drago, E.E., Blettler, M.C.M. & Agostinho, A.A. 2014. Effects of decadal changes in the hydrological regime of the middle reach of the Paraná River (Argentina) on fish densities. *Environmental Biology of Fishes*, 97: 757-771. doi: 10.1007/s10641-013-0177-8
- Feltrin-Contente, R., Freitas-Stefanoni, M. & Gadig, O.B.F. 2009. Size-related shifts in dietary composition of *Centropomus parallelus* (Perciformes: Centropomidae) in an estuarine ecosystem of the southeastern coast of Brazil. *Journal of Applied Ichthyology*, 25: 335-342. doi: 10.1111/j.1439-0426.2008.01179.x
- Fuiman, L., Faulk, A. & Cynthia, K. 2013. Batch spawning facilitates transfer of an essential nutrient from diet to eggs in marine fish. *Biology Letters*, 9: 20130593. doi: 10.1098/rsbl.2013.0593
- García-Vega, A., Fuentes-Perez, J.F., Urretabizkaia, P.M.L., Ganuza, J.A. & Sanz-Ronda, F.J. 2022. Upstream migration of anadromous and potamodromous brown trout: patterns and triggers in a 25-year overview. *Hydrobiologia*, 849: 197-213. doi: 10.1007/s10750-021-04720-9
- González-Félix, M.L., Perez-Velazquez, M., Castellanos-Rico, M., Sachs, A.M., Gray, L.D., Gaines, S.D., et al. 2021. First report on the swim bladder index, proximate composition, and fatty acid analysis of swim bladder from cultured *Totoaba macdonaldi* fed compound aquafeeds. *Aquaculture Reports*, 21: 100901. doi: 10.1016/j.aqrep.2021.100901
- Gracia-Lopez, V., Garcia-Talano, T., Gaxiola-Cortez, G. & Pacheco-Campos, J. 2003. Effect of dietary protein level and commercial feeds on growth and feeding of juvenile common snook, *Centropomus undecimalis* (Bloch, 1792). *Ciencias del Mar*, 29: 585-594.
- Granados-Amores, E., Granados-Amores, J., Zavala-Leal, O.I. & Flores-Ortega, J.R. 2020. Geometric morphometrics in the sulcus acusticus of the sagittae otolith as tool to discriminate species of the genus *Centropomus* (Centropomidae: Perciformes) from the southeastern Gulf of California. *Marine Biodiversity*, 50: 10. doi: 10.1007/s12526-019-01030-1
- Grande, M., Murua, H., Zudaire, I., Arsenault-Pernet, E.J., Pernet, F. & Bodin, N. 2016. Energy allocation strategy of skipjack tuna *Katsuwonus pelamis* during their reproductive cycle. *Journal of Fish Biology*, 89: 2434-2448. doi: 10.1111/jfb.13125
- Guillen, J., Natale, F., Carvalho, N., Casey, J., Hofherr, J., Druon, J.-N., et al. 2019. Global seafood consumption footprint. *Ambio*, 48: 111-122. doi: 10.1007/s13280-018-1060-9
- Habib, S.S., Fazio, F., Naz, S., Arfuso, F., Piccione, G., Rehman, H.U., et al. 2021. Seasonal variations in haematological parameters and body composition of *Labeo rohita* (Rohu) and *Cirrhinus mrigala* (Mrigal Carp) in River Indus, District Dera Ismail Khan, Pakistan. *Turk Journal of Fisheries and Aquatic Sciences*, 21: 435-441. doi: 10.4194/1303-2712-v21_9_02
- Herkenhoff, M.E., Bajay, M.M. & Costamilan, C.A. 2023. Genetic structure and biodiversity in wild *Centropomus parallelus* and in wild and recently domesticated *Centropomus undecimalis* populations. *Life*, 13: 1595. doi: 10.3390/life13071595
- Ibarra-Castro, L. & Duncan, N.J. 2007. GnRH α -induced spawning of wild-caught spotted rose snapper *Lutjanus guttatus*. *Aquaculture*, 272: 737-746. doi: 10.1016/j.aquaculture.2007.09.007
- Jimenez-Martinez, L.D., Alvarez-González, C.A., Tovar-Ramírez, D., Gaxiola, G., Sanchez-Zamora, A., Moyano, F.J., et al. 2012. Digestive enzyme activities during early ontogeny in common snook (*Centropomus undecimalis*). *Fish Physiology and Biochemistry*, 38: 441-454. doi: 10.1007/s10695-011-9525-9
- Li, S., Wen, W., Gong, X., Huang, X. & Chen, N. 2018. Variation of lipids and fatty acids composition in the tissues of wild devil stinger (*Inimicus japonicas*) during sexual maturation. *Aquaculture and Fisheries*, 3: 115-121. doi: 10.1016/j.aaf.2018.05.004
- Maldonado, M., Gracia, V., Kiewek, M., Carrillo, M. & Zanuy, S. 2018. Reproductive cycle of leopard grouper *Mycteroperca rosacea* (Streets, 1877) held in captivity: relationship between gonad development and sex steroid concentration. *Latin American Journal of Aquatic Research*, 46: 83-90. doi: 10.3856/vol46-issue1-fulltext-10
- Maldonado-García, M., Gracia-López, V., Carrillo, M., Hernández-Herrera, A. & Rodríguez-Jaramillo, C. 2005. Stages of gonad development during the reproductive cycle of the blackfin snook, *Centropomus medius* Günther. *Aquaculture Research*, 36: 554-563. doi: 10.1111/j.1365-2109.2005.01253.x
- Martínez-Brown, J.M., Cetzal-Aké, C.A., Ibarra-Castro, L., Sánchez-Cárdenas, R., Maldonado-Amparo, M.A., Rojo-Cebreros, A.H., et al. 2019. Embryonic development of the bullseye puffer *Sphoeroides annulatus* (Tetraodontidae): a morphofunctional approach to ontogenetic steps. *Journal of Morphology*, 280: 948-967. doi: 10.1002/jmor.20994

- McGowan, M.W., Artiss, J.D., Strandbergh, D.R. & Zak, B. 1983. A peroxidase-coupled method for the colorimetric determination of serum triglycerides. *Clinical Chemistry*, 29: 538-542. doi: 10.1093/clinchem/29.3.538
- Medda, A.K., Dasmahapatra, A.K. & Ray, A.K. 1980. Effect of estrogen and testosterone on the protein and nucleic acid contents of liver, muscle, and gonad and plasma protein content of male and female (vitellogenic and nonvitellogenic) Singi fish, *Heteropneustes fossilis* Bloch. *General and Comparative Endocrinology*, 42: 427-436. doi: 10.1016/0016-6480(80)90208-7
- Motta, F.S., Mendonça, J.T. & Moro, P.S. 2016. Collaborative assessment of recreational fishing in a subtropical estuarine system: a case study with fishing guides from southeastern Brazil. *Fisheries Management and Ecology*, 23: 291-302. doi: 10.1111/fme.12172
- Nagahama, Y., Yoshikuni, M., Yamashita, M., Tokumoto, T. & Katsu, Y. 1995. Regulation of oocyte growth and maturation in fish. *Current Topics in Developmental Biology*, 30: 103-145.
- Newman, D.M., Jones, P.L. & Ingram, B.A. 2007. Temporal dynamics of oocyte development, plasma sex steroids, and somatic energy reserves during seasonal ovarian maturation in captive Murray cod *Maccullochella peelii peelii*. *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*, 148: 876-887. doi: 10.1016/j.cbpa.2007.09.001
- Nyuji, M., Hamada, K., Kazeto, Y., Mekuchi, M., Gen, K., Soyano, K., et al. 2018. Photoperiodic regulation of plasma gonadotropin levels in previtellogenic greater amberjack (*Seriola dumerili*). *General and Comparative Endocrinology*, 269: 149-155. doi: 10.1016/j.ygcen.2018.09.007
- Pereira, J.L., Maia, C.M., Chellappa, S., Roubach, R. & Valenti, W.C. 2018. Condition and reproductive aspects of *Leporinus piau* (Fowler) (Characiformes, Anostomidae) in a hypereutrophic reservoir in northeastern Brazil. *Brazilian Journal of Biology*, 78: 78-88.
- Perera-García, M.A., Mendoza-Carranza, M., Contreras-Sánchez, W.M., Huerta-Ortiz, M. & Pérez-Sánchez, E. 2010. Reproductive biology of common snook *Centropomus undecimalis* (Perciformes: Centropomidae) in two tropical habitats. *Revista de Biología Tropical*, 59: 2.
- Peters, K.M., Matheson Jr., R.E. & Taylor, R.G. 1998. Reproduction and early life history of common snook, *Centropomus undecimalis* (Bloch), in Florida. *Bulletin of Marine Science*, 62: 509-529.
- Rivas, L.R. 1986. Systematic review of the perciform fishes of the genus *Centropomus*. *Copeia*, 1986: 579-611. doi: 10.2307/1444940
- Robin, J.H., Regost, C., Arzel, J. & Kaushik, S.J. 2003. Fatty acid profile of fish following a change in dietary fatty acid source: model of fatty acid composition with a dilution hypothesis. *Aquaculture*, 225: 283-293. doi: 10.1016/S0044-8486(03)00296-5
- Rodríguez, L., Zanuy, S. & Carrillo, M. 2001. Influence of daylength on the age at first maturity and somatic growth in male sea bass (*Dicentrarchus labrax*, L.). *Aquaculture*, 196: 159-175. doi: 10.1016/S0044-8486(00)00555-X
- Rodríguez-Barreto, D., Jerez, S., Cejas, J.R., Martín, M.V., Acosta, N.G., Bolaños, A., et al. 2012. Comparative study of lipid and fatty acid composition in different tissues of wild and cultured female broodstock of greater amberjack (*Seriola dumerili*). *Aquaculture*, 360-361: 1-9. doi: 10.1016/j.aquaculture.2012.07.013
- Santos, A.A., Egami, M.I., Ranzani-Paiva, M.J.T. & Juliano, Y. 2009. Hematological parameters and phagocytic activity in fat snook (*Centropomus parallelus*): seasonal variation, sex and gonadal maturation. *Aquaculture*, 296: 359-366. doi: 10.1016/j.aquaculture.2009.08.023
- Sardenne, F., Millot, R., Bessis, E., Puccinelli, E., Bideau, A., Le Grand, F., et al. 2022. Changes in lipid and fatty acid contents of gonad during the reproductive cycle of the Mediterranean swordfish *Xiphias gladius*. *Marine Environmental Research*, 179: 105668. doi: 10.1016/j.marenvres.2022.105668
- Shulman, G.E. & Love, R.M. 1999. *The biochemical ecology of marine fishes*. Academic Press, Cambridge.
- Singh, P.B. & Singh, T.P. 1990. Seasonal correlative changes between sex steroids and lipid levels in the freshwater female catfish, *Heteropneustes fossilis* (Bloch). *Journal of Fish Biology*, 37: 793-802. doi: 10.1111/j.1095-8649.1990.tb02542.x
- Spanopoulos-Zarco, M., Gracia-López, V., Pacheco-Vega, J.M., Estrada-Godínez, J.A., González-Silvera, D., Omont, A., et al. 2022. Reproductive performance of the Pacific red snapper *Lutjanus peru* supplemented with microalgae (*Grammatophora* sp.). *Journal of Applied Phycology*, 34: 395-404. doi: 10.1007/s10811-021-02650-6
- Stickney, D.G. & Torres, J.J. 1989. Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico. *Biología Marina*, 103: 13-24. doi: 10.1007/BF00391060

- Taylor, G.R., Wittington, J.A. & Grier, H.J. 2000. Age growth, maturation and protandric sex reversal in the common snook *Centropomus undecimalis*, from the east and west coasts of south Florida. *Fishery Bulletin*, 98: 612-624.
- Tolussi, C.E., Gomes, A.D., Ribeiro, C., Caneppele, D., Moreira, R.G. & Honji, R.M. 2018. Mobilization of energetic substrates in the endangered catfish *Steindachneridion parahybae* (Siluriformes: Pimelodidae): changes in annual reproductive cycle in captivity. *Neotropical Ichthyology*, 16: 2. doi: 10.1590/1982-0224-20170120
- Tripathi, G. & Verma, P. 2004. Sex-specific metabolic changes in the annual reproductive cycle of a freshwater catfish. *Comparative Biochemistry and Physiology - Part B: Biochemistry & Molecular Biology*, 137: 101-106. doi: 10.1016/j.cbpc.2003.10.005
- Tucker, J.W. 1987. Snook and tarpon snook culture and preliminary evaluation for commercial farming. *The Progressive Fish-Culturist*, 49: 49-57. doi: 10.1577/1548-8640(1987)49<49:SATSCA>2.0.CO;2
- Van Handel, E. 1965. Estimation of glycogen in small amounts of tissue. *Analytical Biochemistry*, 11: 256-265. doi: 10.1016/0003-2697(65)90013-8
- Viader-Guerrero, M., Guzmán-Villanueva, L.T., Spanopoulos-Zarco, M., Estrada-Godínez, J.A., Maldonado-García, D., Gracia-López, V., et al. 2021. Effects of temperature on hatching rate and early larval development of longfin yellowtail *Seriola rivoliana*. *Aquaculture Reports*, 21: 100843. doi: 10.1016/j.aqrep.2021.100843
- Yanes-Roca, C., Rhody, N., Nystrom, M. & Main, K.L. 2009. Effects of fatty acid composition and spawning season patterns on egg quality and larval survival in common snook (*Centropomus undecimalis*). *Aquaculture*, 287: 335-340. doi: 10.1016/j.aquaculture.2008.10.043
- Yeldham, M.I.A., Britton, J.R., Crundwell, C., Davies, P., Dodd, J.R., Nunn, A.D., et al. 2023. Individual repeatability in the timing of river entry indicates the strong influence of photoperiod in the spawning migrations of iteroparous twaite shad *Alosa fallax*. *Hydrobiologia*, 850: 1619-1634. doi: 10.1007/s10750-023-05168-9
- Young, J.M., Yeiser, B.G., Whittington, J.A. & Dutka-Gianelli, J. 2020. Maturation of female common snook *Centropomus undecimalis*: implications for managing protandrous fishes. *Journal of Fish Biology*, 97: 1317-1331. doi: 10.1111/jfb.14475
- Zöllner, N. & Kirsch, K. 1962. Über die quantitative Bestimmung von Lipoiden (Mikromethode) mittels der vielen natürlichen Lipoiden (allen bekannten Plasmalipoiden) gemeinsamen Sulfophosphovanillin-Reaktion. *Zeitschrift für die gesamte experimentelle Medizin*, 135: 545-561. doi: 10.1007/BF02045455
- Zudaire, I., Murua, H., Grande, M., Pernet, F. & Bodin, N. 2014. Accumulation and mobilization of lipids in relation to reproduction of yellowfin tuna (*Thunnus albacares*) in the Western Indian Ocean. *Fisheries Research*, 160: 50-59. doi: 10.1016/j.fishres.2013.12.010

Received: March 31, 2023; Accepted: August 9, 2023