Revista de Biología Tropical, ISSN: 2215-2075, Vol. 74: e2026197, enero-diciembre 2026 (Publicado Mar. 12, 2026)

VERTEBRATE BIOLOGY

REVISTA DE Biología Tropical

https://doi.org/10.15517/j2b2pv90

Gonadal development and sex steroids profile in *Caranx crysos* (Perciformes: Carangidae) in the Colombian Caribbean

Katrina L. Medina-Lambraño[1]; https://orcid.org/0009-0005-5611-5557
Roimer A. Hernández González[1]; https://orcid.org/0009-0001-6518-4301
Alicia Felip Edo[2]; https://orcid.org/0000-0003-4708-9754
Adriana Rodríguez-Forero[1]*; https://orcid.org/0000-0003-1270-5326

1. Grupo de Investigación y Desarrollo Tecnológico en Acuicultura, Laboratorio de Acuicultura Hangar D, Programa de Ingeniería Pesquera. Universidad del Magdalena. Santa Marta, Magdalena, Colombia (ARF); katrinamedinall@unimagdalena.edu.co, roimer.hernandez@aunap.gov.co, arodriguezf@unimagdalena.edu.co, (*Correspondence)
2. Consejo Superior de Investigaciones Científicas (CSIC), Grupo de Fisiología de la Reproducción de Peces, Instituto de Acuicultura Torre de la Sal, Ribera de Cabanes s/n, 12595, Castellón, España; afelip@iats.csic.es

Received 03-VII-2025. Corrected 14-X-2025. Accepted 26-II-2026.

ABSTRACT

Introduction: *Caranx crysos* holds significant importance as a source of income for local communities in the Colombian Caribbean region. There is a scarcity of information regarding this species, particularly concerning its reproductive biology.

Objectives: To evaluate reproductive indicators related to gonadal development, thereby establishing a reference point for both management and the regulation of reproduction in controlled systems, as well as for aquaculture purposes.

Methods: To achieve this, fish were collected monthly, in Taganga Bay (Colombia), over a year with the assistance of local artisanal fishermen. Biometric data were recorded, and fluctuations in plasma estradiol and testosterone levels were analyzed in relation to changes in the gonadosomatic index (GSI).

Results: The highest GSI values in females were recorded from May to July, while males showed a significant increase in GSI between June and July. In females, plasma levels of 17β-estradiol peaked in May and June before declining in July ($p < 0.05$). Testosterone levels in males were elevated from May to July, remaining lower yet stable from August to March. Oocyte development was asynchronous, with mature oocytes observed from February to July, while mature males were present from July to September.

Conclusions: These results suggest that the reproductive season of *C. crysos* (the blue runner) spans from late spring to early autumn, the optimal period to start artificial reproduction assessments.

Key words: aquaculture; *Caranx crysos*; gonadal development; reproduction; sex steroids.

RESUMEN

Desarrollo gonadal y perfil de esteroides sexuales de *Caranx crysos* (Perciformes: Carangidae) en el Caribe colombiano

Introducción: *Caranx crysos* tiene una importancia significativa como fuente de ingresos para las comunidades locales en la región del Caribe colombiano. Existe escasez de información sobre esta especie, particularmente sobre su biología reproductiva.

Objetivos: Evaluar indicadores reproductivos relacionados con el desarrollo gonadal, estableciendo así un punto de referencia tanto para el manejo y la regulación de la reproducción en sistemas controlados, como para fines acuícolas.
Métodos: Se recolectaron peces mensualmente durante un año, en la Bahía de Taganga (Colombia), con la ayuda de pescadores artesanales locales. Se registraron datos biométricos y se analizaron las fluctuaciones en los niveles plasmáticos de estradiol y testosterona en relación con los cambios en el índice gonadosomático (IGS).
Resultados: Los valores más altos de IGS en las hembras se registraron de mayo a julio, mientras que los machos mostraron un aumento significativo del IGS entre junio y julio. En las hembras, los niveles plasmáticos de 17β-estradiol alcanzaron su punto máximo en mayo y junio antes de disminuir en julio ($p < 0.05$). Los niveles de testosterona en los machos se elevaron de mayo a julio y permanecieron más bajos pero estables de agosto a marzo. El desarrollo de los ovocitos fue asincrónico, observándose ovocitos maduros de febrero a julio, mientras que los machos maduros estuvieron presentes de julio a septiembre.
Conclusiones: Estos resultados sugieren que la temporada reproductiva de *C. crysos* se extiende desde finales de primavera hasta principios de otoño, el período óptimo para iniciar las evaluaciones para el control de su reproducción artificial.

Palabras clave: acuicultura; *Caranx crysos*; desarrollo gonadal; reproducción; esteroides sexuales.

INTRODUCTION

The blue runner (*Caranx crysos*) (Mitchill, 1815), commonly known as "cojinoa" in the Colombian Caribbean, is a crucial source of income and nutrition for rural families in the region. Notably, its fishing yield reached 1 577.1 metric tons along the Colombian Caribbean coast in 2020 (Duarte, et al., 2022). Despite the significant commercial and economic value of *C. crysos*, there is a lack of information concerning its reproductive biology. Previous research has investigated various reproductive parameters of the blue runner, such as body weight and length, size at first maturity, sex ratio, gonadosomatic index, fecundity, and spawning season (Assem, 2000; Figuerola-Fernández et al., 2008; Goodwin & Finucane, 1985; Oliveira et al., 2017; Sley et al., 2012). Nevertheless, further studies are necessary to clarify specific reproductive traits. This gap in knowledge poses a significant challenge to the effective management and sustainable use of the species, especially regarding the expansion of marine aquaculture in Latin America and the Caribbean (Muñiz et al., 2022; Piferrer et al., 2023).

Studies show that the blue runner displays an extended and geographically diverse reproductive season, which demonstrates its significant reproductive plasticity. This variation is influenced by changes in abiotic factors, including temperature, food supply, and the seasonal variations between dry and wet periods. For instance, the size at which first maturity occurs (L_{50}) shows considerable variation across various regions: Specifically, males in the Gulf of Gabes (Tunisia) reached sexual maturity at a fork length of 210.20 mm, while females achieved maturity at 222.3 mm (Sley et al., 2012). In contrast, the blue runner in the Coastal Waters of Rio Grande do Norte, Brazil, first reaches sexual maturation at a total body length of 331 mm for both sexes, whereas blue runners from the Eastern Gulf of Mexico showed a maturity length of 267 mm (Goodwin & Finucane, 1985).

Understanding the reproductive biology and life history strategies of *C. crysos* is essential for the successful implementation of fishery management, conservation initiatives, and aquaculture practices. Consequently, detailed information on reproductive biology is crucial for assessing population health, estimating biomass, and understanding the relationship between fish condition, lipid storage, and gonadal development (Vazzoler & Rossi-Wongtschowski, 1976).

The global demand for fishery products is driving the expansion of aquaculture, and Latin America is emerging as a significant producer

(Mechaly et al., 2023). However, a significant challenge exists in the mass production of marine fish, primarily due to the scarcity in the controlled production of high-quality eggs and larvae. Consequently, their cultivation largely relies on the fattening of juveniles sourced from the natural environment. In order to facilitate the regulated reproduction of these fish, it is crucial to undertake studies into the reproductive biology, physiology, and endocrinology of these species.

Nowadays, *C. crysos* is considered a potential species of interest in aquaculture in the Caribbean area as this carangid species has wide acceptance in local and regional markets (Rombenso et al., 2014). For this reason, the analysis of reproductive parameters of blue runner specimens from the Taganga Bay (Monoguaka bay, Santa Marta, Colombia), is essential for a medium-short-term vision of rural areas as it can contribute to the assessment of the state of exploitation of the stocks. Altogether, it could guarantee a proper use of the resource in the wild and captivity conditions thus assisting with United Nations Sustainable Development Goals including zero hunger (SDG2) and life below water (SDG14). Our hypothesis suggests that the reproduction of *C. crysos* follows a seasonal pattern in the Colombian Caribbean, with a reproductive peak occurring between May and July. This pattern of heightened activity is directly reflected in the fluctuations of key indicators such as the gonadosomatic index (GSI), gonadal histology, and plasma concentrations of sex steroids (estradiol and testosterone).

MATERIAL AND METHODS

Study area and fish sampling: A total of 117 fish specimens were collected from the catch landings of artisanal longline fisheries in Monowaka bay, Taganga Bay (11°16’12” N & 74°11’57” W over a one-year period, from June to May 2018-2019). These specimens were transported rapidly to the Aquaculture Laboratory facilities at the Universidad del Magdalena in Santa Marta, Colombia. The handling of the animals adhered to the guidelines for the care and use of laboratory animals established by the University of Magdalena. Prior to each sampling, the fish were anesthetized using clove oil (eugenol 4-Allyl-2-Methoxyphenol) at doses of 0.1 ml l^{-1}. The total length of each fish was measured to the nearest 0.1 cm, and their weight was recorded using a digital balance with a precision of 0.01 g (Navigator, OHAUS). The total length and weight data of females and males was grouped into class intervals of 2 cm and 47 g, respectively according to Anderson and Neumann (1996). The length-weight relationship (i.e., isometric *vs* positive or negative allometric growth) was determined by the equation:

$$W = a\ [TL]^b$$

Where, W is the body weight (g) of fish, TL is the total length (cm), a is the intersection and b is the coefficient of growth or regression index (Froese, 2006). The condition factor (K) was calculated by the equation:

$$K = W\ [TL^3) \times 100]$$ (Nash et al., 2006).

When necessary, fish were sacrificed using an overdose of anesthetic and gonad and liver samples were quickly removed and weighed for the calculation of the GSI and hepatosomatic (HSI) indexes according to the following equations:

$$GSI= (Gonad\ weight)/W \times 100 \text{ and } HIS = (Liver\ weight)/W \times 100.$$

Steroid analysis: Blood samples were collected from the caudal vein, using heparinized syringes and 21-gauge needles. Plasma was separated by centrifugation at 3 578 g and 4 °C for 15 minutes and stored at -80 °C until analyzed. Circulating plasma steroid levels of testosterone (T) and 17β-estradiol (E_2) were measured using a commercial microplate chemiluminescence enzyme immunoassay (Acculite CLIA Microwells (Monobind Inc.®), employing the testosterone (3 775-300) and estradiol (4 975-300)

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 74: e2026197, enero-diciembre 2026 (Publicado Mar. 12, 2026)

kit systems, respectively). Quantitative determination of T and E_2 concentration in plasma was determined by a microplate chemiluminescence reader (LumiStat 4100 de Awareness Technology®). The detection limits were 130 pg/g for T and 30 pg/g for E_2. Inter- and intra-assay coefficients of variability were 9.3 and 6.1 % for T and 3.5 and 3.3 % for E_2.

Histological analysis: A small piece of gonad (< 0.1 g) was fixed for 24 h in 10 % neutral buffered formalin for histological analyses (Copper et al., 2018). These pieces were dehydrated by a graded ethanol series, embedded in paraffin wax, cut into 5 µm sections, and then stained with haematoxylin-eosin (H-E). Samples were examined under the conventional light microscope (Carl Zeiss) and photographic recording with a digital camera (AxionCam ERc5S) to identify the types of germ cells and characterize the stage of gonadal development according to the criteria described by Viette et al. (1997). All specimens were sorted by sex as males (M) or females (F) in each sampling point.

Statistical analysis: All data are presented as mean ± SD, and assessments of normality and homoscedasticity were conducted prior to analysis using Shapiro-Wilk and Levene tests, respectively. Statistical tests were executed using Statgraphics Technologies, Inc. (2025) Centurion version 1.18, while graphical representations were created with the SIGMAPLOT software package version 11 and Excel version 2403. Frequency graphs and one-way ANOVA tests were utilized to examine sex differences as well as variations between and within sampling months concerning weight and length. A Person correlation analysis was conducted to explore the relationship between weight and length, and the potential growth pattern of the species was assessed through a length-weight linear regression, and significant differences between the slopes were evaluated using a Student's t-test. Additionally, a chi-square test (χ^2) was performed to assess the sex ratio, with a significance level set at 5 %. The GSI, HSI, K, and plasma levels of E_2 were analyzed using one-way ANOVA tests and the Multiple Range Test, while the plasma levels of T were assessed using a nonparametric Kruskal-Wallis test.

RESULTS

Biometric measurements of male and female *C. crysos*: A total of 58 males and 59 females were examined in this study. The distribution of total length and weight classes of males and females is shown in Fig. 1. All captured fish measured over 20 cm in total length (Fig. 1A) and weighed 141.9 g (Fig. 1B). The total length of females ranged from 24.2 to 40.9 cm, with weights between 141.9 and 646.6 g (Fig. 2A, Fig. 2B). In contrast, males exhibited a total length ranging from 25.1 to 42 cm and weights from 169.6 to 614.6 g (Fig. 2C, Fig. 2D). Significant differences in growth performance were identified in terms of length (F = 5.95 and 7.67, $p < 0.05$) and body weight (F = 7.38 and 10.98, $p < 0.05$) for both females and males across the sampled months (Fig. 2). In addition, a significantly different length-weight relationship was observed between males and females of the blue runner from Taganga Bay ($p < 0.05$) (Fig. 3). This relationship showed a coefficient of determination (r^2) of 0.870 for males and 0.934 for females. The length-weight relationship for males was expressed as $W = 0.046TL^{2.58}$, while for females, it was $W = 0.0129TL^{2.9526}$. These findings indicated an isometric growth pattern ($b = 3$) for *C. crysos* ($t = -1.254$, $p = 0.214$). The monthly distribution of occurrence frequencies for both males and females revealed no significant differences in the sex ratio, which remained at 1 M:1 F ($\chi^2 = 8.27$, $p > 0.05$) (Fig. 4). However, a notable prevalence of females was recorded in July (Fig. 4A). While 30.51 % of females and 46.55 % of males were found within the size range of 30.2 to 32.2 cm, a higher proportion x 44 of females (61.02 %) was identified in the size classes spanning from 30.2 to 34.2 cm (Fig. 4B).

Seasonal changes in GSI, HSI and K: The highest value of GSI of > 1.22 % in females

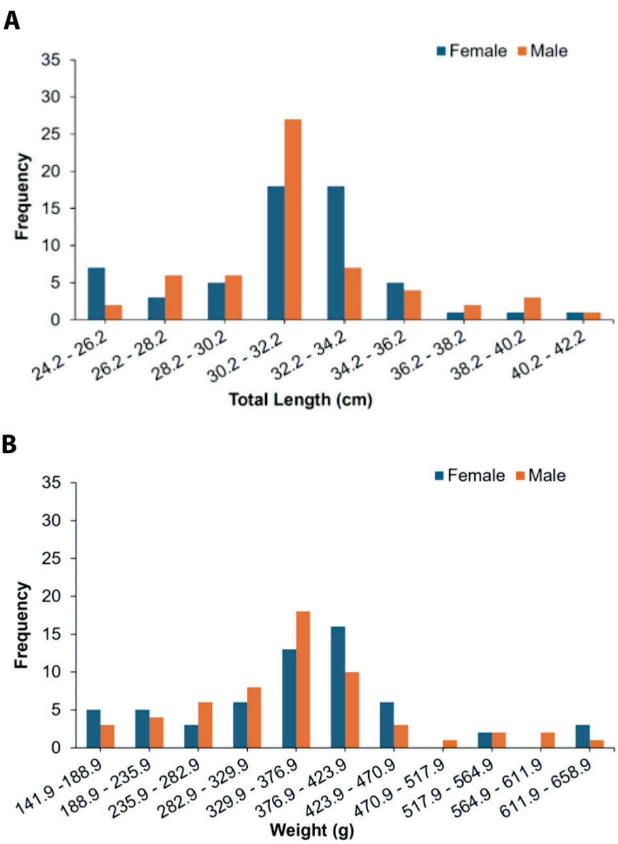

Fig. 1. Size distribution frequency of female (orange vertical bars) and male (blue vertical bars) blue runner (*Caranx crysos*) (N = 117 fish) from the Taganga Bay in the Colombia´s Caribbean coast. **A.** Total length. **B.** Total body weight

was observed in May, June and July (Fig. 5A). The GSI decreased significantly in August and maintained low from September to February. Then, GSI values progressively increased until May, presenting significant monthly variations (Multiple Range Tests, $p < 0.05$) (Fig. 5A). From June to October, the HSI presented values around (1.11 ± 0.33, 1.09 ± 0.09, 1.00 ± 0.17, 1.18 ± 0.23, 0.99 ± 0.14 %) respectively and then significantly decreased in November (0.76 ± 0.11 %) (Fig. 5B). From December onwards, HSI values progressively increased with maximum values in March (1.35 ± 0.35 %) and then significantly decreased in May (1.05 ± 0.27 %). Variations of K showed that significant statistical differences were observed between the sampling months (Multiple Range Tests, $p < 0.05$) (Fig. 5C). Females showed maximum values of K in June (1.09 ± 0.16), September (1.18 ± 0.03) and March (1.10 ± 0.13) (Fig. 5C). In the case of males, monthly variation of GSI showed significant statistical differences (Multiple Range Tests, $p < 0.05$) with maximum values in June (2.08 ± 0.92 %) and July (2.2 ± 1.14 %) which progressively decreased in December (0.30 ± 0.19 %) (Fig. 5D). Values of GSI remained low and a slight increase was observed in May (1.16 ± 0.38 %), presenting significant monthly variations (Multiple Range Tests, $p < 0.05$) (Fig. 5D). The HSI presented values around (0.97 ± 0.19, 0.94 ± 0.05, 0.87 ± 0.17, 1.11 ± 0.15, 0.95 ± 0.12 %) between the months of June to October respectively and then significantly decreased in November (0.71 ± 0.14 %)

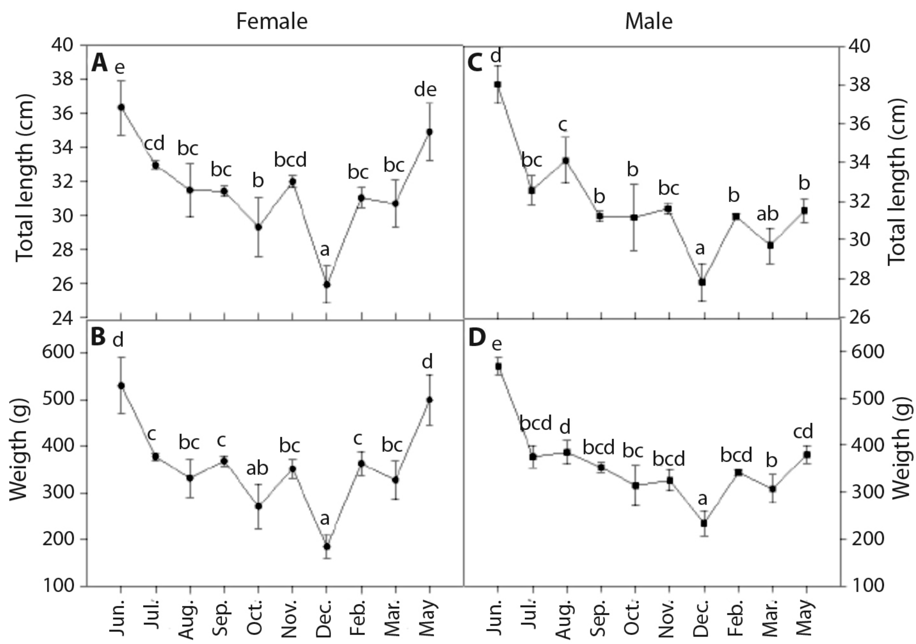

Fig. 2. Total length and body weight (mean ± standard error) of female and male of *Caranx crysos* from the Taganga Bay in the Colombia´s Caribbean coast. **A.** Total length female. **B.** Total weight female. **C.** Total length male. **D.** Total weight male.

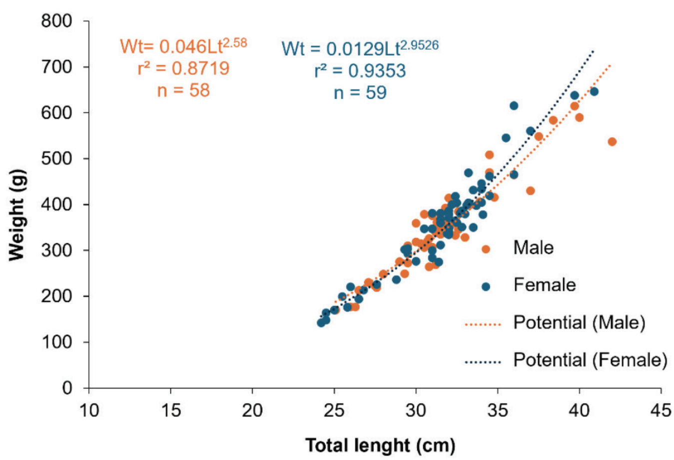

Fig. 3. Length-weight relationship for males and females of *Caranx crysos* captured (N = 117) during the study period from the Taganga Bay in the Colombia´s Caribbean coast.

and December (0.85 ± 0.17 %) (Fig. 5E). The HSI values increased in February (1.15 ± 0.23 %) and remained unchanged until July. The minimum values of HSI coincided with the lower GSI values in both sexes in November. In males, the maximum and minimum values of K were found in May (1.21 ± 0.09) and August (0.97 ± 0.12), respectively, presenting significant monthly variations (Multiple Range Tests, $p < 0.05$) (Fig. 5F) (Table 1).

Histological characterization of gonadal development of *C. crysos*: The ovarian developmental stages of female blue runners are

Table 1
Estimated parameters of the sex-ratio, body size (length and weight), size range, length-weight relationship, growth type and size at first sexual maturity for *Caranx crysos* from different geographical areas including the Taganga Bay in the Colombia´s Caribbean coast (this study).

Geographic Area	Sex	Sex ratio (M:F)	Length (mm)		Weight (g)		Length-Weight relationship			Size at first sexual maturity (mm)	Reference
			Min	Max	Min	Max	r^2	Equation	Growth type		
Bay of Taganga, Monoguaka, Santa Marta - Colombia	Female	1 :1	242	409	141.9	646.6	0.93	$W = 0.0129TL^{2.9526}$	Isometric (b = 3)	340	This study
	Male		251	420	169.6	614.6	0.87	$W = 0.046TL^{2.58}$			
Rio Grande do Norte (Northeastern Brazil)	Female	1:1.1	230	480	136	1 040	0.916	$W = 0.0346TL^{2.6717}$	n.d.	331 (L_{50})	Oliveira et al. (2017)
	Male		283	435	168	843					
Gulf of Gabes (Southern Tunisia)	Female	1:0.87	99		8.3	855	n.d.	n.d.	n.d.	210.2 ± 0.6 (FL_{50})	Sley et al. (2012)
	Male		95		8.7	880	n.d.	n.d.	n.d.	222.3 ± 0.4 (FL_{50})	
South Florida		1:1.15	270	460	295	1 816					
Northwest Florida	Female	1:1.66	242	272	288	475	n.d.	n.d.	n.d.	267	Goodwin & Finucane, (1985)
Mississippi Delta		1:1.91	304	304	505	1 362					

Abbreviations: n.d, not reported.

shown in Fig. 6. The ovaries were categorized into five developmental stages: i) the perinucleolar stage, characterized by oocytes with a prominent nucleus and multiple nucleoli (Fig. 6A), ii) the cortical alveoli stage, which features oocytes containing lipid droplets within the cytoplasm (Fig. 6B), iii) the vitellogenesis stage, where oocytes increase in size and accumulate lipid droplets (Fig. 6C), and iv) the maturation stage (Fig. 6D), marked by further enlargement of the oocytes, the presence of yolk granules and lipid droplets, as well as the visibility of the zona radiata and the perivitelline space. The ovarian development stages of *C. crysos* throughout its annual life cycle were assessed (Fig. 7A). The findings indicated that as oocyte development progressed from February to July, females exhibited oocytes undergoing vitellogenesis, characterized by an increase in size and the presence of lipid droplets, along with a discernible zona radiata and perivitelline space, indicative of maturation. The highest percentage of maturing females was recorded between May and July, suggesting that the breeding season for the blue runner predominantly occurs during the summer months in Taganga Bay. In males, two phases of testicular development were identified. These phases included individuals with mature tests (Fig. 8A) and those with regressed tests (Fig. 8B). During the mature phase, the testes contained a full spectrum of male germ cells, such as spermatogonia A and B, primary spermatocytes, and spermatids, which had undergone transformation into spermatozoa, occupying the inner regions of the lobe (Fig. 8A). Conversely, the fish exhibiting regressed tests showed residual spermatozoa and connective tissue was visible and in turn, spermatogenesis ceased (Fig. 8B).

Seasonal changes in hormone plasma levels of *C. crysos*: Plasma E_2 concentrations in females were elevated in June, followed by a gradual decline starting in July (Fig. 9A). An increase in plasma E_2 levels was noted in October, continuing to rise until May, which corresponded with the peak occurrence of sexual maturation in females, characterized by oocytes

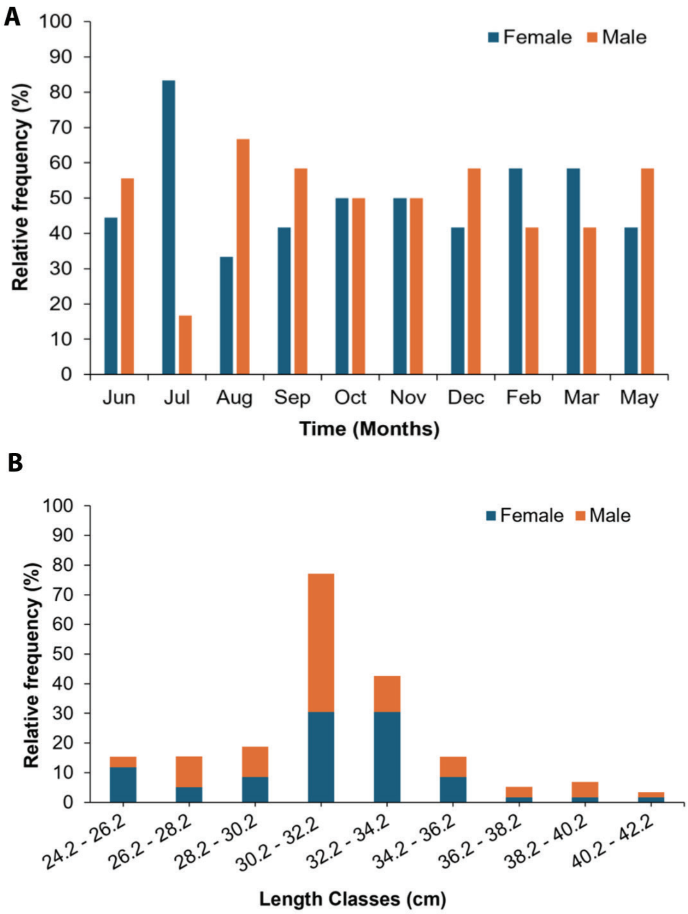

Fig. 4. Relative frequency of monthly values. **A.** Length classes. **B.** Sex ratio of *Caranx crysos* from the Taganga Bay in the Colombia´s Caribbean coast. Female: orange vertical bars. Male: blue vertical bars.

in the vitellogenic and maturation stages (Kruskal-Wallis test, $p < 0.05$). In males, higher plasma T levels were recorded during May, June, and July. Subsequently, T levels decreased in August and remained low until March, when a rise was observed, although this increase was not statistically significant compared to the preceding month (Fig. 9B). In summary, T levels were notably high during the summer months, aligning with the highest percentage of males displaying maturing testes (Fig. 7B).

DISCUSSION

Managing the reproduction of potential aquaculture species presents a significant challenge in formulating fishery management strategies. This is essential for establishing specific protocols and procedures that address the development of aquaculture in Latin America and the Caribbean, ultimately enhancing fish production and preventing resource depletion (Muñiz et al., 2022; Piferrer et al., 2023). Our

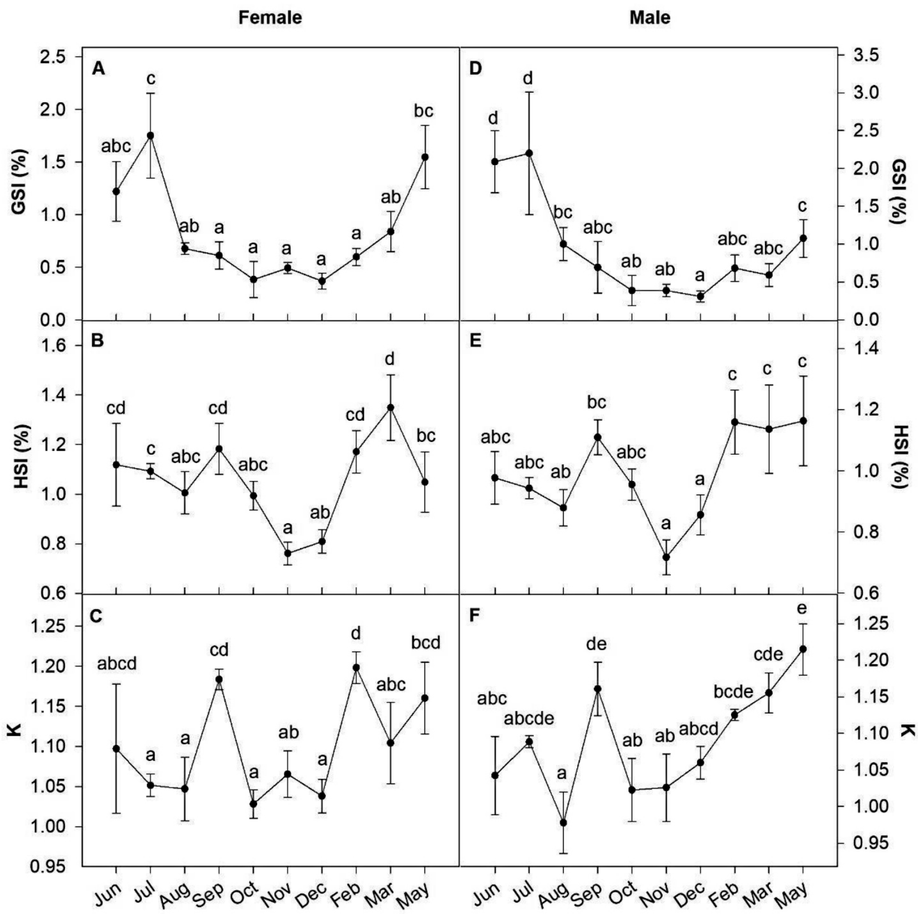

Fig. 5. Temporal variation (mean ± standard error) in gonadosomatic index (GSI), hepatosomatic index (HSI) and condition factor (K) of female. (**A**-**B**-**C**) and male (**D**-**E**-**F**) respectively, of *Caranx crysos* from Taganga Bay. N = 117.

findings showed that the size at sexual maturity for *C. crysos* collected from Taganga Bay was approximately 340 mm, which aligns with findings reported for specimens from Northeastern Brazil (Oliveira et al., 2017). In contrast to those reported for fish found around the Gulf of Gabes in Tunisia (males: 210.20 cm, and females: 222.3 cm). This variation could be attributed to the application of different methodologies, temporal sampling differences, and changes in morphometric and physiological assessments. In this sense, enhanced collaboration in fisheries research, along with the establishment of standardized methodologies for determining size at first maturity, could significantly contribute to effective fishery management and stock assessment for commercially valuable species (Haig et al., 2016).

This study reports a balanced sex ratio of 1:1, throughout the annual cycle which aligns with findings from blue runner populations in Northeastern Brazil and Southern Tunisia (Oliveira et al., 2017; Sley et al., 2012). In contrast, a skewed sex ratio favoring females has been observed in Northwest and South Florida, as well as the Mississippi Delta (Goodwin & Finucane 1985; Table 1). Such variations in sex ratio may be attributed to selective capture practices based on the size and sex of the fish, among other influencing factors (Oliveira et al., 2017;

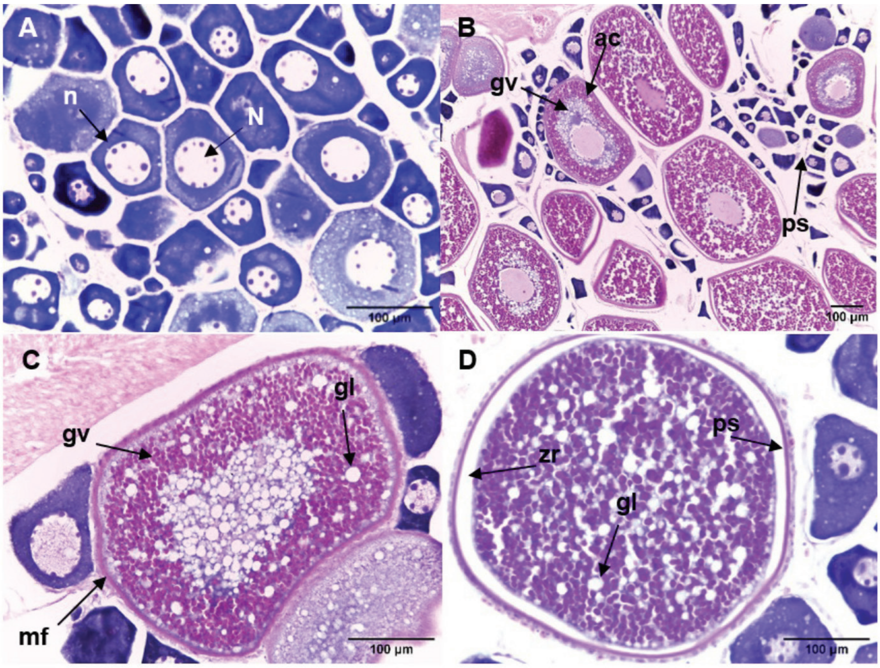

Fig. 6. Ovarian stages in females of *Caranx crysos*. **A.** Oocyte in perinucleolar phase. The nucleus (N), with numerous nucleoli (n) (40X). **B.** Oocyte in alveolus-cortical phase. Note the cortical alveolus (ac) at the cell periphery, yolk granules (gv) and some perinucleolar oocytes are visible (1) (10X). **C.** Oocyte in vitellogenesis phase showing an increase in oocyte volume. The yolk granules (gv), lipid droplets (gl), and the follicular membrane (mf) are visible (40X). **D.** Oocyte in the maturation phase showing the zona radiata (zr), lipid droplets (gl) and the perivitelline space (ps) (40X).

Sley et al., 2012). In *C. crysos*, a gonochoric species, the size-selective fishing does not directly alter the sex of individuals; however, the spatial segregation between males and females may create biases in the captured sex ratio. Variations in maturity size, differential habitat use, and seasonal migrations can lead to the overexploitation of one sex, particularly females, thereby compromising reproductive capacity and distorting population assessments. These biases pose a risk to fishery management, as they may result in ineffective conservation strategies, hinder the population's ability to recover, affect the future recruitment of the species, and threaten the sustainability of the resource (Alonzo & Mangel, 2004; Goodwin & Finucane, 1985; Hutchings, 2004; Oliveira et al., 2017; Sley et al., 2012).

Our research indicates that the blue runner exhibits an isometric growth pattern, as previously reported (Jobling, 2002). In contrast, individuals of the same species captured in the Gulf of Gabes (Southern Tunisia, Central Mediterranean) displayed isometric growth (Ghailen et al., 2010). This discrepancy implies that various factors may affect the length-weight relationship in fish, such as growth stage, sex, seasonal variations, food availability, maturity level, and overall fish condition (i.e., health status) (Ghailen et al., 2010). For fisheries and aquaculture, a fish exhibiting isometric growth facilitates management and enhances predictability. It simplifies the estimation of a fish's weight based on its length, which is crucial for evaluating the total biomass of a fish stock and forecasting the yield of a catch. This uniformity also enables the development of more accurate fishing gear, which can minimize bycatch. In aquaculture, isometric growth streamlines growth monitoring, making it easier to optimize

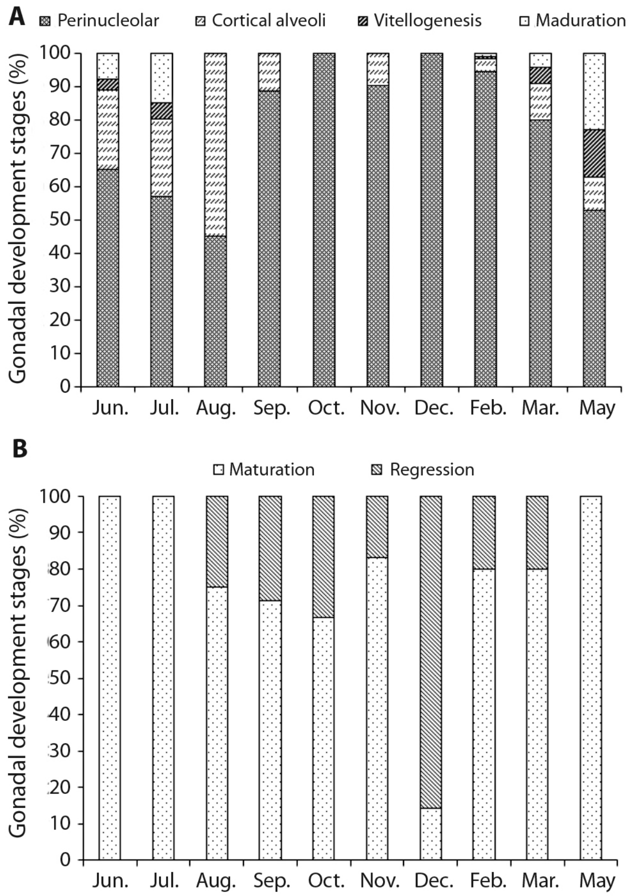

Fig. 7. Rates of the gonadal development stages over a year. **A.** Female (N = 59). **B.** Male (N = 58). *Caranx crysos* from the Taganga Bay in the Colombia´s Caribbean Coast.

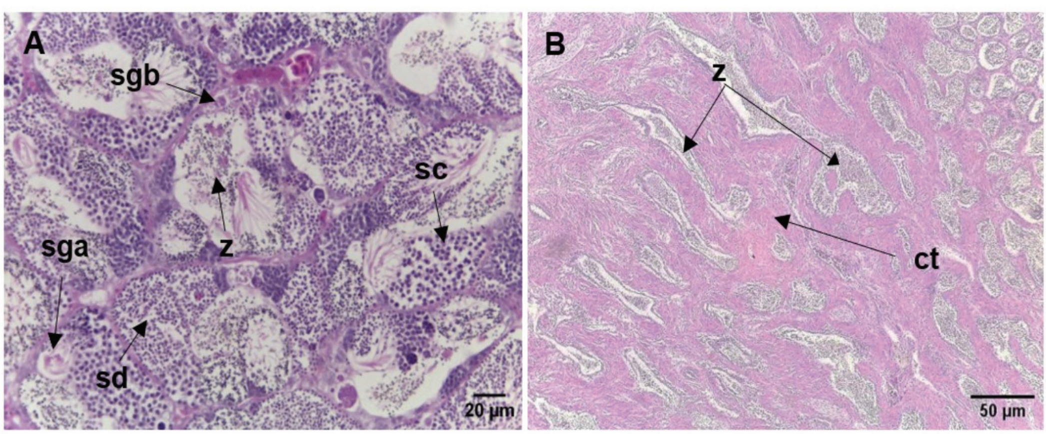

Fig. 8. Testicular stages in males of *Caranx crysos*. **A.** Mature testis showed type A and B spermatonia (sga, sgb), primary spermatocytes (sc), spermatids (sd) and spermatozoa (z) (40X). **B.** Regressed testicle exhibiting spermatozoa (z) and connective tissue (ct).

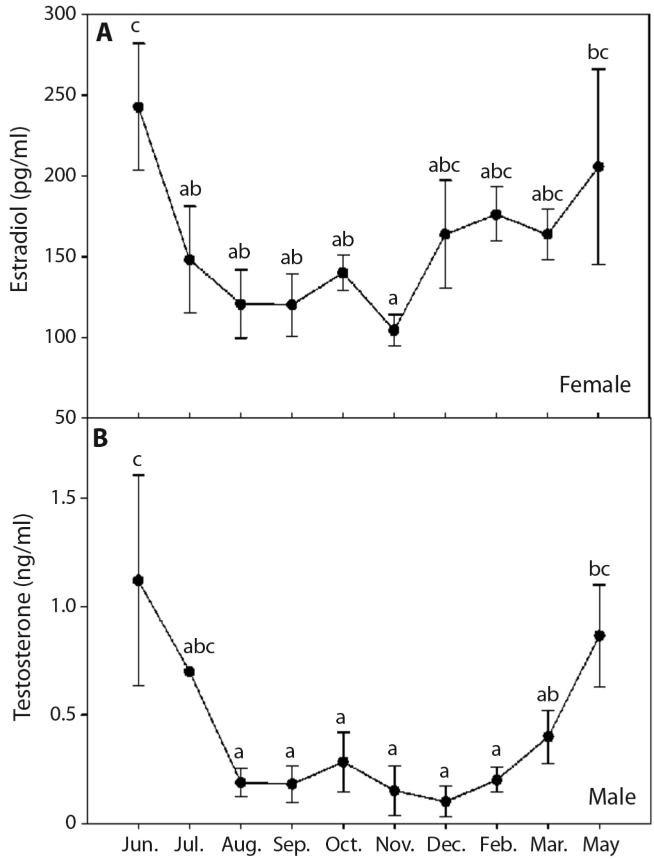

Fig. 9. Seasonal profile of plasma 17β-estradiol (E_2) **(A)** and testosterone (T) **(B)** of female and male of *Caranx crysos* (N = 117), respectively, from the Taganga Bay in the Colombia´s Caribbean coast. Each value represents mean ± standard deviation. Different letters indicate significant differences ($p < 0.05$).

feeding schedules, model feed conversion rates (FCR), alleviate stress on the fish, and enhance economic efficiency (Li et al., 2021; Mazumder et al., 2016).

The condition factor values for female ranged from 1.02 ± 0.04 to 1.19 ± 0.05, while male exhibited values between 0.97 ± 0.12 and 1.21 ± 0.09. These findings suggest a favorable state of health for the fish sampled throughout various life cycle stages (Clarito, 2021). Notably, a decline in the condition factor was recorded during the summer months, which coincided with peak GSI values observed in blue runners within Taganga Bay. Conversely, lower GSI values were associated with reduced HSI values, indicating a significant correlation between gonadal development patterns and HSI in this species. The findings align with those presented by Smith (1997), indicating that the breeding season for the species may occur between May and July, during which histological analyses revealed the highest proportions of mature males and females. The connections between GSI, HSI, and K offer a distinct understanding of the balance between reproduction and survival in the blue runner. During the breeding season, fish allocate significant resources to the production of gametes, a process that depletes their energy reserves. As the GSI increases, reflecting heightened reproductive activity, both the HSI and the K decrease. This indicates that the fish are exhausting essential lipid reserves stored in their liver and experiencing a reduction in overall body weight to support reproduction, highlighting a crucial trade-off between reproductive success and physical health. Following spawning, a fish's main priority transitions to recover and the restoration of energy reserves. It is essential for them to consume substantial amounts of food to restore lipids and protein depleted during the reproductive process. A fish that does not sufficiently recover is at a greater risk of predation and may even skip spawning in subsequent years as a result of its compromised physical condition (Birnie-Gauvin et al., 2023; McBride et al., 2015; Sharma & Ram, 2020).

It is important to note that this breeding period could extend from January to August, as maximum values of the GSI have been recorded from February to October, with notable peaks occurring in May and June (Figuerola-Fernández et al., 2008; Oliveira et al., 2017; Sley et al., 2012). The observed variations in the reproductive behavior of blue runner fish may be linked to geographic factors influenced by changes in abiotic conditions, including temperature, precipitation, and food supply (Wen & Lin, 2001). The gonadal development cycle of *C. crysos* exhibits a pattern comparable to that of the horse mackerel, *Seriola lalandi lalandi* (Poortenaar et al., 2001), and the bluefin horse mackerel, *Caranx melampygus* (Moriwake et al., 2001), characterized by a relatively extended spawning period during the vitellogenesis phase for this species.

Gonadal growth and development in fish are known to be regulated by the brain-pituitary-gonad axis (Zohar et al., 2010). This study has elucidated the relationship between key reproductive parameters, such as E_2 in females and T in males, and their correlation with changes in HSI, gonadosomatic index GSI, and various stages of gonadal development in wild blue runner specimens along the Caribbean coast of Colombia. Histological analyses revealed the presence of oocytes at various developmental stages within the ovaries of this species. These findings suggest that the blue runner exhibits a multiple spawning strategy, characterized by asynchronous oocyte development in females, a reproductive adaptation observed in several other fish species, including Mediterranean amberjack (*Seriola dumerilii*) (Marino et al., 1995), yellowtail kingfish (*S. lalandi lalandi*) (Poortenaar et al., 2001), Bluefin trevally (*C. melampygus*) (Moriwake et al., 2001), and common dentex (*Dentex dentex*) (Loir et al., 2001), as well as previously described in blue runner (Goodwin & Finucane, 1985; Oliveira et al., 2017).

In this study, observations of female blue runners showed that as oocyte development progresses many cortical alveoli are replaced by yolk proteins in the later stages of oocyte development, resulting in their relocation to the periphery of the oocyte, adjacent to the radiate zone (Mylonas et al., 2004; Oliveira et al., 2017). Regarding the seasonal fluctuations in plasma levels of E_2 and T, elevated concentrations were noted during the initial phases of gonadal maturation. The peak levels of E_2 corresponded with periods of increased reproductive activity among female fish, while the lowest concentrations of E_2 were recorded in August, September, and November, coinciding with the presence of previtellogenic oocytes. These results suggest that, similar to other fish species, E_2 levels in blue runners rise during vitellogenesis and subsequently decline during the final maturation phase (Ohta et al., 2001; Sisneros et al., 2004). On the other hand, testosterone levels increased during active spermatogenesis, whereas T concentrations remained low from August to February, indicating a considerable proportion of individuals entering a regressive stage.

In conclusion these findings indicate that the reproductive cycle of *C. crysos* is predominantly influenced by seasonal factors. This assumption is supported by noteworthy correlations observed between hormonal fluctuations and trends in biological indices, which thereby affirms our initial hypothesis. Our findings presented are significant not only for the formulation of fisheries management strategies but also for contributing valuable insights relevant to conservation initiatives and the management practices concerning blue runner populations. In this sense, further studies are necessary to highlight endocrine and molecular control mechanisms of fish reproduction (Lubzens et al., 2010; Miura & Miura 2003; Schulz et al., 2010; Yaron & Levavi-Sivan, 2011). Such investigations aim to enhance our understanding of the reproductive physiology of wild *C. crysos*, thereby establishing a foundational reference for the regulation of reproduction in controlled environments with the aim of initiating fish farming programs.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

This research was funded through internal resources of the Research and Technological Development Group in Aquaculture (GIDTA) and by the project *"Estudio para la caracterización y ensayos de reproducción en peces de importancia comercial del departamento del Magdalena con fines de conservación y manejo*" affiliated with the Vice-Rectorate for Research at the University of Magdalena (Santa Marta, Colombia). Additional support was provided through the CSIC scientific cooperation program for development (i-COOP; COOPA20482) awarded to Alicia Felip and Adriana Rodríguez Forero.

REFERENCES

Alonzo, S. H., & Mangel, M. (2004). The effects of size-selective fisheries on stock dynamics and sperm limitation in sex-changing fish. *Fishery Bulletin, 102*(1), 1–14.

Anderson, R. O., & Neumann, R. M. (1996). Length, weight, and associated structural indices. In B. R. Murphy, & D. R. Willis (Eds.), *Fisheries techniques* (pp. 447–481). American Fisheries Society.

Assem, S. (2000). The reproductive biology and histological characteristics of pelagic carangid female Caranx crysos from the Egyptian Mediterranean Sea. *Journal of the Egyptian German Society of Zoology, 31*(C), 195–215.

Birnie-Gauvin, K., Berthelsen, C., Larsen, T., & Aarestrup, K. (2023). The physiological costs of reproduction in a capital breeding fish. *Physiological and Biochemical Zoology, 96*(1), 40–52. https://doi.org/10.1086/722136

Clarito, Q. Y. (2021). Length–weight relationship and relative condition factor of yellowstripe scad, Selaroides leptolepis (Cuvier, 1833) in the Visayan Sea, Philippines. *Aceh Journal of Animal Science, 6*(3), 74–78. https://doi.org/10.13170/ajas.6.3.20220

Copper, J. E., Budgeon, L. R., Foutz, C. A., van Rossum, D. B., Vanselow, D. J., Hubley, M. J., Clark, D. P., Mandrell, D. T., & Cheng, J. C. (2018). Comparative analysis of fixation and embedding techniques for optimized histological preparation of zebrafish. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology, 208*, 38–46. https://doi.org/10.1016/j.cbpc.2017.11.003

Duarte, L. O., Cuervo, C., Vargas, O., Gil-Manrique, B., Tejeda, K., De León, G., Isaza, E., Cuello, F., Curiel, J., Manjarrés-Martínez, L., & Reyes-Ardila, H. (2022). *Estadísticas de desembarco y esfuerzo de las pesquerías artesanales de Colombia 2021* (Informe técnico). Autoridad Nacional de Acuicultura y Pesca; Universidad del Magdalena.

Figuerola-Fernández, M., Peña-Alvarado, N., & Torres-Ruiz, W. (2008). *Aspects of the reproductive biology of recreationally important fish species in Puerto Rico* (Federal Assistance Project F-48). U.S. Fish and Wildlife Service.

Froese, R. (2006). Cube law, condition factor and weight–length relationship: History, meta-analysis and recommendations. *Journal of Applied Ichthyology, 22*(4), 241–253. https://doi.org/10.1111/j.1439-0426.2006.00805.x

Ghailen, H., Abdallah, H., Hassan, A., Mourad, C., Abderrahmen, B., & Othman, J. (2010). Length–weight relationships for 13 fish species from the Gulf of Gabes (southern Tunisia, central Mediterranean). *African Journal of Biotechnology, 9*(37), 6177–6181.

Goodwin, J., & Finucane, J. (1985). Reproductive biology of blue runner *Caranx crysos* from the eastern Gulf of Mexico. *Northeast Gulf Science, 7*(2), 139–146. https://doi.org/10.18785/negs.0702.02

Haig, J. A., Bakke, S., Bell, M. C., Bloor, I. S. M., Cohen, M., Coleman, M., Dignan, S., Kaiser, M. J., Pantin,

J. R., Roach, M., Salomonsen, H., & Tully, O. (2016). Reproductive traits and factors affecting the size at maturity of Cancer pagurus across northern Europe. *ICES Journal of Marine Science, 73*(10), 2572–2585. https://doi.org/10.1093/icesjms/fsw081

Hutchings, J. A. (2004). The cod that got away. *Nature, 428*(6986), 899–900. https://doi.org/10.1038/428899a

Jobling, M. (2002). Environmental factors and rates of development and growth. In P. J. B. Hart, & J. D. Reynolds (Eds.), *Handbook of fish biology and fisheries* (pp. 97–122). Blackwell Science.

Li, L., Shen, Y., Yang, W., Xu, X., & Li, J. (2021). Effect of different stocking densities on fish growth performance: A meta-analysis. *Aquaculture, 544*, 737152. https://doi.org/10.1016/j.aquaculture.2021.737152

Loir, M., Le Gac, F., Somarakis, S., & Pavlidis, M. (2001). Sexuality and gonadal cycle of the common dentex (Dentex dentex) in intensive culture. *Aquaculture, 139*(3–4), 366–381. https://doi.org/10.1016/S0044-8486(00)00514-7

Lubzens, E., Young, G., Bobe, J., & Cerdà, J. (2010). Oogenesis in teleosts: How fish eggs are formed. *General and Comparative Endocrinology, 165*, 367–389. https://doi.org/10.1016/j.ygcen.2009.05.022

Marino, G., Mandich, A., Massari, A., Andaloro, F., Porrello, S., Finola, M. G., & Cevasco, F. (1995). Aspects of reproductive biology of the Mediterranean amberjack (Seriola dumerili) during the spawning period. *Journal of Applied Ichthyology, 11*, 9–24. https://doi.org/10.1111/j.1439-0426.1995.tb00002.x

Mazumder, S. K., Das, S. K., Bakar, Y., & Ghaffar, M. A. (2016). Effects of temperature and diet on length–weight relationship and condition factor of the juvenile Malabar blood snapper (Lutjanus malabaricus). *Journal of Zhejiang University-SCIENCE B, 17*(8), 580–590. https://doi.org/10.1631/jzus.B1500250

McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., & Basilone, G. (2015). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries, 16*(1), 23–57. https://doi.org/10.1111/faf.12043

Mechaly, A. S., Batlouni, S. R., Elisio, M., Sanches, E. A., Chacon, J., Maldonado, M., Rodríguez-Forero, A., Vissio, P., Fatsini, E., Nuñez, J., & Duncan, N. (2023). Spawning induction for Latin American fishes. *Reviews in Aquaculture, 16*, 337–356. https://doi.org/10.1111/raq.12841

Miura, T., & Miura, C. I. (2003). Molecular control mechanisms of fish spermatogenesis. *Fish Physiology and Biochemistry, 28*, 181–186. https://doi.org/10.1023/B:FISH.0000030522.71779.47

Moriwake, A. M., Moriwake, V. N., Ostrowski, A. C., & Lee, C. S. (2001). Natural spawning of the bluefin trevally Caranx melampygus in captivity. *Aquaculture, 203*(1–2), 159–164. https://doi.org/10.1016/S0044-8486(01)00621-4

Muñiz, R. M. J., Jimber del Río, J. A., Jiménez, B. F. J., & Vera, G. P. (2022). The fisheries and aquaculture sector in Latin America: Exports to East Asia and production. *PLOS ONE, 17*(7), e0267862. https://doi.org/10.1371/journal.pone.0267862

Mylonas, C. C., Papandroulakis, N., Smboukis, A., Papadaki, M., & Divanach, P. (2004). Induction of spawning of cultured greater amberjack (Seriola dumerili) using GnRHa implants. *Aquaculture, 237*(1–4), 141–154. https://doi.org/10.1016/j.aquaculture.2004.04.015

Nash, R. D. M., Valencia, H. A., & Geffen, A. (2006). The origin of Fulton's condition factor: Setting the record straight. *Fisheries, 31*(5), 236–238.

Ohta, K., Mine, T., Yamaguchi, A., & Matsuyama, M. (2001). Steroidogenic pathway to estradiol-17β synthesis in the ovarian follicles of the protogynous wrasse Pseudolabrus sieboldi. *Zoological Science, 18*, 937–945. https://doi.org/10.2108/zsj.18.937

Oliveira, M., Nóbrega, M., Oliveira, J., & Chellappa, S. (2017). Reproductive biology of blue runner Caranx crysos from the coastal waters of Rio Grande do Norte, Brazil. *Journal of Aquaculture & Marine Biology, 5*(6), 00136. https://doi.org/10.15406/jamb.2017.05.00136

Piferrer, F., Felip, A., Saavedra, C., Rotllant, G., Yúfera, M., Pérez-Sánchez, J., Fernández, J., Valdebenito, I., Rodríguez-Forero, A., Fernandes, B., López-Greco, L., Rosas, C., Lazo, J. P., & Villamil, L. (2023). *Recomendaciones para la gestión de los recursos acuáticos en Latinoamérica y el Caribe.* Agencia Española de Cooperación Internacional para el Desarrollo.

Poortenaar, C., Hooker, S., & Sharp, N. (2001). Assessment of yellowtail kingfish (Seriola lalandi lalandi) reproductive physiology as a basis for aquaculture development. *Aquaculture, 201*, 271–286. https://doi.org/10.1016/S0044-8486(01)00549-X

Rombenso, A., Bowzer, J., Moreira, C., & Sampaio, L. (2014). Culture of Caranx species in near-shore cages off the Brazilian coast during colder months. *Aquaculture Research, 47*, 1687–1690. https://doi.org/10.1111/are.12629

Schulz, R. W., de França, L. R., Lareyre, J. J., Le Gac, F., Chiarini-Garcia, H., Nóbrega, R. H., & Miura, T. (2010). Spermatogenesis in fish. *General and Comparative Endocrinology, 165*(3), 390–411. https://doi.org/10.1016/j.ygcen.2009.02.013

Sharma, L., & Ram, R. N. (2020). Relationship of gonadosomatic and hepatosomatic indices in two age groups of common carp. *International Journal of Current*

Microbiology and Applied Sciences, 9(3), 727–732. https://doi.org/10.20546/ijcmas.2020.903.087

Sisneros, J. A., Forlano, P. M., Knapp, R. H., & Bass, A. H. (2004). Seasonal variation of steroid hormone levels in an intertidal-nesting fish, the vocal plainfin midshipman. *General and Comparative Endocrinology, 136*(1), 101–116. https://doi.org/10.1016/j.ygcen.2003.12.007

Sley, A., Jarboui, O., Ghorbel, M., & Bouain, A. (2012). Annual reproductive cycle, spawning periodicity and sexual maturity of blue runner Caranx crysos. *Journal of Applied Ichthyology, 28*, 785–790. https://doi.org/10.1111/j.1439-0426.2012.02039.x

Smith, C. (1997). *National Audubon Society field guide to tropical marine fishes*. Alfred A. Knopf.

Statgraphics Technologies, Inc. (2025). *Statgraphics Centurion* (Versión 19.7.01) [Software estadístico]. https://www.statgraphics.com/download19

Vazzoler, A. E. A. de M., & Rossi-Wongtschowski, C. L. D. B. (1976). Sardinella brasiliensis: Tipo de desova, fecundidade e potencial reprodutivo relativo. *Boletim do Instituto Oceanográfico, 25*, 131–155. https://doi.org/10.1590/S0373-55241976000200001

Viette, M., Giulianini, P. G., & Ferrero, E. A. (1997). Reproductive biology of scad Trachurus mediterraneus from the Gulf of Trieste. *ICES Journal of Marine Science, 54*, 267–272. https://doi.org/10.1006/jmsc.1996.0185

Wen, H., & Lin, H. (2001). Effect of environmental factors on gonadal maturation, ovulation, and spawning in teleosts. *The Journal of Applied Ecology, 12*(1), 151–155.

Yaron, Z., & Levavi-Sivan, B. (2011). Hormonal control of reproduction and growth. In A. P. Farrell (Ed.), *Encyclopedia of fish physiology* (pp. 1500–1508). Academic Press. https://doi.org/10.1016/B978-0-12-374553-8.00058-7

Zohar, Y., Muñoz-Cueto, J. A., Elizur, A., & Kah, O. (2010). Neuroendocrinology of reproduction in teleost fish. *General and Comparative Endocrinology, 165*(3), 438–455. https://doi.org/10.1016/j.ygcen.2009.04.017