Neotropical Ichthyology

Original article

https://doi.org/10.1590/1982-0224-2026-0097

Reproductive tactics and trophic ecology of *Ophisternon aenigmaticum* (Synbranchiformes: Synbranchidae) in a Neotropical Mexican lake

Correspondence:
Osiris Valerio-Mendoza
osiris.valeriom@gmail.com

Nayeli Gonzalez-Rodriguez[1] and Osiris Valerio-Mendoza[2,3]

The reproductive tactics and trophic ecology of the swamp eel *Ophisternon aenigmaticum* were evaluated over a seasonal cycle in Lake Catemaco, Mexico. Analysis of 242 specimens revealed a persistent male-biased sex ratio of 2.72:1. Quantitative stomach content analysis using the numerical abundance method demonstrated a hyper-piscivorous specialization, with fish accounting for 98.76% of the cumulative diet across the rainy and dry seasons. This finding refutes the paradigm characterizing Neotropical synbranchids as opportunistic benthic generalists. Morphometric and macroscopic classifications confirmed a six-stage ovarian trajectory and a four-stage testicular dynamic. The population exhibited a bimodal reproductive strategy synchronized with regional precipitation, displaying prominent gonadosomatic index (GSI) peaks during late autumn (November) and mid-summer (June-July). Gravid females exhibited low absolute fecundity (353.86 ± 67.69 oocytes) but produced remarkably large, yolk-rich telolecithal eggs (up to 4.5 mm). This trade-off supports an equilibrium life-history model designed to maximize larval survival and burrowing success in dynamic Neotropical lacustrine environments.

Keywords: Apex predator, Catemaco, Eel-like fishes, Reproductive strategies, Stomach content.

Submitted June 16, 2026
Accepted August 21, 2026
Epub ???, 2026

Associate Editor Evelyn Habit
Section Editor Fernando Pelicice
Editor-in-chief José Birindelli

1 Departamento de Morfología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Prolongación de Carpio y Plan de Ayala s/n, Casco de Santo Tomás, 11340 Ciudad de México, Mexico. nayeli.patologia@gmail.com.

2 Instituto de Biología, Departamento de Zoología, Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Circuito Exterior s/n, Ciudad Universitaria, 04510 Ciudad de México, Mexico. osiris.valeriom@gmail.com (corresponding author).

3 Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León, Carretera Nacional km 145, 67700 Linares, Nuevo León, Mexico.

Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 24, no. 4, 2026

Se evaluaron las tácticas reproductivas y la ecología trófica de la anguila de pantano *Ophisternon aenigmaticum* durante un ciclo de temporadas en el Lago de Catemaco, México. El análisis de 242 especímenes reveló una proporción sexual persistente sesgada hacia los machos de 2.72:1. El análisis cuantitativo del contenido estomacal mediante el método de abundancia numérica demostró una especialización hiper-piscívora, donde los peces representaron el 98.76% de la dieta acumulada en las temporadas de lluvias y secas. Este hallazgo refuta el paradigma que caracteriza a los sinbránquidos neotropicales como generalistas bentónicos oportunistas. Las clasificaciones morfométricas y macroscópicas confirmaron una trayectoria ovárica de seis etapas y una dinámica testicular de cuatro etapas. La población exhibió una estrategia reproductiva bimodal sincronizada con la precipitación regional, mostrando picos prominentes del índice gonadosomático (IGS) durante el final del otoño (noviembre) y la mitad del verano (junio-julio). Las hembras grávidas exhibieron una baja fecundidad absoluta (353.86 ± 67.69 oocitos) pero produjeron huevos telolecitos notablemente grandes y ricos en vitelo (hasta 4.5 mm). Este balance respalda un modelo de historia de vida de equilibrio diseñado para maximizar la supervivencia larvaria y el éxito de enterramiento en ambientes lacustres neotropicales dinámicos.

Palabras clave: Catemaco, Contenido estomacal, Depredador ápice, Estrategias reproductivas, Peces con forma de anguila.

INTRODUCTION

The order Synbranchiformes comprises highly evolved, eel-like freshwater and brackish water teleosts primarily distributed throughout tropical and subtropical wetlands. Within this order, the family Synbranchidae, commonly known as swamp eels, exhibits remarkable anatomical, ecological, and physiological adaptations to survive in extreme, hypoxic environments, including specialized respiratory strategies and burrowing mechanisms. Anatomically, these fishes are characterized by an elongated body, the complete absence of pectoral and pelvic fins, and dorsal and anal fins reduced to rayless ridges (Das, 2023). A primary diagnostic feature of Synbranchidae is the confluence of the gill openings across the throat, forming a single transverse ventral slit (Mar-Silva *et al*., 2022). Furthermore, species within this family lack a functional gas bladder and scales, relying on specialized tissues for respiratory gas exchange outside the water column (Paschoal *et al*., 2024). Currently, the group represents a vital component of both paleotropical and neotropical aquatic biodiversity, displaying significant taxonomic complexity and wide ecological variation across diverse lineages (Mar-Silva *et al*., 2022; Das, 2023; Paschoal *et al*., 2024).

Within the Neotropical region, the genus *Ophisternon* is represented by highly specialized lineages, with Mexico acting as the northernmost limit of its geographical distribution (Mar-Silva *et al*., 2022). While some species within this genus are restricted to subterranean systems, *Ophisternon aenigmaticum* occurs in a variety of epigean freshwater environments, including wetlands, slow-flowing rivers, and shallow lakes

across Mexico, Cuba, and Central America (Fricke *et al*., 2026). Despite this widespread regional presence and its documented role as a targeted small-scale fishery resource for human consumption in local lacustrine communities, fundamental knowledge regarding the life-history traits of this species is critically lacking. Most contemporary research on Neotropical synbranchids has focused heavily on South American lineages, leaving a profound baseline data deficit for populations in North America (Mar-Silva *et al*., 2022). Consequently, comprehensive data concerning the ecological niche, trophic interactions, and population dynamics of *O. aenigmaticum* remain completely uncharacterized in the current literature, hindering the development of reliable conservation and management frameworks.

From an evolutionary and ecological perspective, understanding the life-history strategies of lineages within Synbranchidae provides crucial insights into trophic web dynamics and population sustainability in species-rich Neotropical environments (Albert *et al*., 2020). In lacustrine ecosystems characterized by high levels of endemism, such as Lake Catemaco, evaluating trophic ecology clarifies the regulatory role of key predators on native fish communities, particularly regarding sympatric populations of Poeciliidae. Moreover, although *O. aenigmaticum* has been regionally characterized as a protogynous hermaphrodite, theoretical models of protogyny typically predict female-biased populations or strict size-structured transitions (Casas, Saborido-Rey, 2021; Chong-Montenegro, Kindsvater, 2022). Therefore, documenting population structures that deviate from these classical expectations represents a significant challenge to understanding the reproductive plasticity of synbranchids.

To resolve these demographic asymmetries, evaluating seasonal sex ratios and structural variations becomes critical to unraveling the ecological or behavioral mechanisms driving demographic asymmetries in Neotropical ecosystems. Seasonal fluctuations of the gonadosomatic index (GSI) and macro-morphometric gonadal structures can thus be used to track demographic shifts and reproductive investment under this life-history framework (Albert *et al.,* 2020; Paschoal *et al*., 2024). These quantitative biological parameters are essential for identifying potential structural responses to localized anthropogenic exploitation. Ultimately, analyzing the synchronization between dietary adjustments and bimodal reproductive outputs in the northernmost range of the family provides a baseline framework that complements the broader biological knowledge established for South American synbranchids (Mar-Silva *et al*., 2022; Paschoal *et al*., 2024).

Therefore, we determined the dietary composition and characterized the reproductive parameters of *O. aenigmaticum* within its northernmost geographical range in Lake Catemaco, Veracruz, Mexico. Specifically, we evaluated the seasonal variations in the diet of this species using the numerical abundance method to characterize its trophic composition and document predation on sympatric populations of the endemic poeciliids *Poeciliopsis catemaco* and *Poecilia catemaconis*. Concurrently, we described the gonadal maturity cycle, established specialized macroscopic scales for both ovaries and testes, tracked seasonal fluctuations of the total and sex-specific GSI, and estimated both absolute and relative fecundity. Through this comprehensive approach, this work provides the first integrated ecological baseline required to support sustainable fishery regulations, seasonal bans, and conservation initiatives for this poorly known Neotropical swamp eel.

MATERIAL AND METHODS

Study area. Fieldwork was conducted in the Lake Catemaco region, located in the southern territory of the state of Veracruz, Mexico. The lake is situated at an altitude of 340 m above sea level, with its geographic center positioned at coordinates 18°25'34"N 95°06'45" W (Secretaría de Marina, 2022). This complex lacustrine ecosystem is characterized by specific limnological dynamics and tropical climate variations (Muciño-Márquez *et al*., 2021). The region exhibits significant seasonal fluctuations in precipitation and environmental erosion that directly influence the ecological resilience of coastal zones and freshwater systems in Veracruz (Silva *et al*., 2023). Collections were localized specifically around the littoral environments of Agaltepec Island, an area characterized by dense marginal vegetation and muddy substrates.

Biological sampling and examined material. Systematic sampling was conducted monthly over a 10-month period from October 2024 to July 2025, strategically capturing the full seasonal environmental dynamics of the region across two representative macro-seasons: the rainy season (comprising October-November 2024 and June-July 2025) and the dry season (extending from December 2024 to May 2025). Taxonomic classification and identification of the target species followed the standard reference of Fricke *et al*. (2026). A total sample of 242 specimens of *Ophisternon aenigmaticum* was collected, comprising 177 males and 65 females, reflecting the active structure and availability of populations of this species within the evaluated microhabitats across the described seasonal windows. To ensure scientific reproducibility and allow future verification, all 242 collected specimens were fixed in 10% formalin, preserved in 70% ethanol, and formally deposited as single cataloged lot in the Colección de Especímenes del laboratorio de Patología de la Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, under the official catalog identifier ENCB-CP-05, following the international acronym standards established by Sabaj (2020).

Stomach content and diet analysis. To quantitatively evaluate the dietary composition of this species, the complete digestive tract was dissected, and stomach contents were extracted and examined fresh immediately following euthanasia to prevent post-mortem autolysis and ensure optimal taxonomic identification of prey items. Quantitative analysis was subsequently performed using the Numerical Abundance Method (%N) following standard protocols for fish stomach content analysis and individual feeding niche variations (Kang *et al*., 2025; Sánchez-Hernández *et al*., 2025). This metric was calculated using the following mathematical formulation:

$$\%N = (\eta_i/\Sigma\eta) * 100$$

Where η_i represents the total number of individuals belonging to a specific prey category i, and $\Sigma\eta$ represents the cumulative number of all prey items identified across the entire analyzed sample. To evaluate potential seasonal shifts in food resource exploitation, this quantitative index was calculated separately for both the rainy and dry seasons.

Fish processing and gonadal analysis. Following collection, specimens were ethically euthanized via thermal shock in an ice-water bath (hypothermia) to minimize distress, maintaining strict adherence to international animal welfare standards for handling target teleosts. This procedure, along with the complete experimental protocol, was formally reviewed and approved by the Institutional Bioethics Committee of the Escuela Nacional de Ciencias Biológicas (ENCB-IPN) under the official registration code ZOO/02/11.

In the laboratory, each organism was morphometrically evaluated by measuring total length (TL, to the nearest 0.1 cm) and total weight (TW, to the nearest 0.01 g) using a digital caliper and a precision electronic balance, respectively. Sex determination was performed through a ventral incision followed by direct macroscopic examination of the gonads based on the morphological criteria of Martín-Montero *et al.* (2024). Sex was macroscopically assigned based on distinct diagnostic characteristics: females were differentiated by turgid, granular, and heavily vascularized ovaries displaying yellowish to orange coloration and larger relative volume; males were identified by slender, smooth, ribbon-like testes with a firm texture and whitish to light-cream coloration; transitional or intersex individuals were characterized by intermediate gonadal structures exhibiting mixed pale pink coloration and reduced lobulation.

To classify the gonadal developmental phases, individual gonads were detached, weighed, and examined under a stereomicroscope. Maturity stages were determined based on the macroscopic evaluation criteria and gonadosomatic relationships validated by Quispe-Salazar *et al.* (2025). Considering these optical observations and variations in shape, color, weight, and volume, a reproductive macroscopic maturity scale was adapted for *Ophisternon aenigmaticum* (Tab. **S1**). This framework comprised six macroscopic stages for females (Stages II to VII) and four macroscopic stages for males (Stages II to V); notably, immature individuals corresponding to Stage I were not detected for either sex during the study period.

Gonadosomatic index and fecundity estimations. To quantify the seasonal energetic investment in reproduction, the Gonadosomatic Index (GSI) was calculated for every individual using the following standard formulation:

$$GSI = (W_g/W_t) * 100$$

Where W_g represents the wet weight of the gonad (g) and W_t represents the total body weight of the fish (g). To evaluate if reproductive allocation was synchronized with environmental variations, the mean Gonadosomatic Index (GSI) was calculated as $GSI = (W_g/W_t) * 100$, where W_g represents wet gonad weight (g) and W_t represents total body weight (g). Differences in GSI values across the local macro-seasons defined by regional rainfall periods (rainy *vs.* dry; Costa *et al.*, 2026) were statistically analyzed using non-parametric Mann-Whitney U tests.

Fecundity estimations were restricted strictly to females displaying advanced gonadal maturity (Stage VI; see Tab. **S1**). Absolute fecundity was determined through the direct total counting of all vitellogenic oocytes present in both ovaries, which were gently separated using fine dissection needles and quantified under a Nikon SMZ-1B stereomicroscope. Relative fecundity was subsequently calculated as the total number of mature oocytes produced per gram of female body weight.

Statistical analyses. Data normality and homogeneity of variance were evaluated using Shapiro-Wilk and Levene's tests, respectively. Because data deviated from a normal distribution, non-parametric statistics were utilized. Differences in GSI values and dietary composition across seasons and sexes were tested using Mann-Whitney U tests, whereas variations across operational maturity stages were evaluated using Kruskal-Wallis H tests followed by Dunn's post-hoc tests. Deviations from a 1:1 sex ratio were assessed using Chi-square (χ^2) goodness-of-fit tests. Linear regression analyses were performed to evaluate the relationships between female body dimensions (total body weight Wt) and reproductive metrics (absolute fecundity). To quantitatively evaluate dietary specialization and feeding strategy, Shannon's diversity index (H') and Levins' standardized trophic niche breadth (Ba) were calculated based on numerical dietary proportions (%N). Continuous biological variables are presented as mean ± standard error (SE) and 95% confidence intervals (95% CI). All statistical procedures were executed in R software (v. 4.3.1), with significance set at $\alpha = 0.05$.

RESULTS

Population structure and environmental relations. A total of 242 specimens of *Ophisternon aenigmaticum* were successfully collected and evaluated across the studied cycle, comprising 177 males and 65 females (Tab. 1). The baseline demographic analysis revealed a persistent male-biased sex ratio throughout the entire investigation (Chi-square test: $\chi^2 = 51.83$, df = 1, $p < 0.0001$), displaying an overall cumulative ratio of 2.72:1 (M: F). A direct seasonal comparison showed that this male bias remained consistently elevated across climatic regimes without seasonal inversion. Specifically, when segregated by seasonal windows, the dry season yielded the highest concentration of captures (N = 171), maintaining a sex ratio of 2.64:1 (M:F; $\chi^2 = 33.74$, $p < 0.0001$) , with December 2024 exhibiting the most pronounced male dominance at 5.86:1 (M:F; $\chi^2 = 23.02$, $p < 0.0001$) (Tab. 1). Conversely, the rainy season accounted for 71 collected individuals, representing a highly skewed sexual proportion of 2.94:1 (M:F; $\chi^2 = 18.21$, $p < 0.0001$), driven primarily by a sharp drop in female availability observed during June 2025.

Dietary composition and seasonal trophic ecology. Quantitative evaluation of the stomach contents demonstrated an extraordinary degree of dietary specialization in *O. aenigmaticum* within Lake Catemaco. The numerical abundance method (%N) identified fish as the absolute dominant prey category, accounting for 98.76% of the cumulative global diet (Tab. 1). Taxonomic screening of this prey items revealed the explicit presence of the endemic poeciliids *Poeciliopsis catemaco* and *Poecilia catemaconis*, confirming focused predation on the native lacustrine ichthyofauna.

This hyper-piscivorous behavior remained virtually unchanged across seasonal environmental fluctuations, registering total values of 100% numerical abundance in eight out of the ten monitored months. Alternative taxonomic categories of prey items were critically scarce (mollusks: 0.83% N; crustaceans: 0.41% N) and restricted to minor opportunistic encounters. Trophic diversity indices confirmed an extreme degree of dietary specialization; Shannon's diversity index yielded a remarkably low overall value of H' = 0.072 (H'rainy = 0.218; H'dry = 0.129), while Levins' standardized trophic

TABLE 1 | Seasonal variation in the dietary composition of *Ophisternon aenigmaticum* in Lake Catemaco, Veracruz, Mexico, based on the Numerical Abundance Method (%N). Within the "Fish" prey category, specimen fragments were taxonomically identified as the endemic poeciliids *Poeciliopsis catemaco* and *Poecilia catemaconis*.

Season / Month	Predators collected (N)	Sex ratio (M:F)	Prey category	Number of prey (η_i)	Numerical abundance (%N)	Total orey per period ($\Sigma\eta$)
Rainy season	71	2.94:1	–	–	–	71
October 2024	17	3.25:1	Fish Mollusks	16 1	94.12 5.88	17
November 2024	23	2.28:1	Fish	23	100.00	23
June 2025	15	4.00:1	Fish	15	100.00	15
July 2025	16	3.00:1	Fish	16	100.00	16
Dry season	171	2.64:1	–	–	–	171
December 2024	48	5.86:1	Fish	48	100.00	48
January 2025	36	2.00:1	Fish	36	100.00	36
February 2025	18	3.50:1	Fish	18	100.00	18
March 2025	33	1.20:1	Fish Crustaceans Mollusks	31 1 1	93.94 3.03 3.03	33
April 2025	18	3.50:1	Fish	18	100.00	18
May 2025	18	3.50:1	Fish	18	100.00	18
Total Pool	242	2.72:1	Fish Crustaceans Mollusks	239 1 2	98.76 0.41 0.83	242

niche breadth was close to zero (Ba = 0.012; Barainy = 0.038; Badry = 0.021). These metrics quantitatively demonstrate a narrow, specialized piscivorous feeding niche with minimal seasonal shift in resource utilization (Tab. 1).

Gonadal maturity cycles. The macroscopic and morphometric classifications of gonadal development in *O. aenigmaticum* are detailed in Tab. 2. Female gonadal maturation followed a six-stage operational trajectory spanning from immature to spent phases (Stages II to VII). Immature ovaries (Stage II; mean weight = 0.61 g, mean length = 144.08 mm) exhibited a distinct pink coloration and an unformed, thickened tegument with no visible oocytes. As development progressed toward advanced phases, the ovaries transitioned to well-defined cylindrical morphologies, shifting from yellowish-orange granular structures in Stage III (Developing) (mean weight = 1.24 g, mean length = 130.50 mm) to thick, clearly yellow or orange robust structures in Stage IV (Maturing) (mean weight = 2.35 g, mean length = 137.54 mm), characterized by larger and completely opaque vitellogenic oocytes. The subsequent Stage V (Mature) (mean weight = 7.15 g, mean length= 131.52 mm) and Stage VI (Gravid) (mean weight = 11.75 g, mean length= 152.37 mm) phases were structurally characterized by a progressively thinning, translucent ovarian wall due to distension, heavily packed with large vitellogenic telolecithal oocytes. Finally, post-spawning dynamics were verified by a single regressed female in Stage VII (Spent; weight = 0.50 g, length = 151.78 mm), which macroscopically presented completely flaccid, collapsed, and brownish-red hemorrhagic ovaries with an absolute reduction in tissue volume and only a few residual oocytes undergoing reabsorption.

In contrast, male testicular development was categorized into four stages, showing an asymmetric growth pattern where the left testis was consistently more developed than the right. Immature testes (Stage II; mean weight = 0.42 g, mean length = 134.31 mm) lacked distinct coloration or defined geometry. Developing testes (Stage III; mean weight = 0.91 g, mean length= 134.43 mm) turned pink and assumed a characteristic pyramidal shape in cross-section. At full maturity (Stage IV; mean weight = 1.96 g, mean length= 151.79 mm), the paired structures fused into a single, cohesive testicular mass with a milky-white coloration, covered by a brownish-spotted tegument. Fully regressed or spent testes (Stage V; mean weight = 0.27 g, mean length= 136.76 mm), characterized by a distinct brownish-red coloration and an absolute loss of turgor, were abundant during post-spawning periods. The macroscopic and morphometric classifications of gonadal development in *O. aenigmaticum* are detailed in Tab. **S1** and summarized in Tab. 2. The minimum total length (TL) at first gonadal maturity was highly synchronized between sexes, recorded at 414 mm for females (Stage VI; Tab. 2) and 415 mm for males (Stage IV; Tab. 2).

Reproductive seasonality and gonadosomatic index (GSI). The population displayed a clearly defined bimodal reproductive strategy closely synchronized with regional environmental variations. Gravid females (Stage VI) and mature males (Stage IV) were exclusively present during two distinct reproductive windows: a secondary pulse occurring late in the year (November to January, associated with late rainfall events) and a highly synchronized, primary peak during the onset of the main rainy season (June and July). During March 2025, mature stages were entirely absent from the population, coinciding with a dominant pulse of immature (Stage II) individuals.

TABLE 2 | Morphometric parameters and sample size (N) across the different operational gonadal maturity stages of *Ophisternon aenigmaticum* in Lake Catemaco, Veracruz, Mexico. Range values in parentheses.

Sex	Maturity stage	N	Mean gonad weight (g)	Mean gonad length (mm)	Mean gonad width (mm)
Females		65			
	Stage II (Immature)	11	0.61 (0.38–0.95)	144.08 (108.02–164.00)	2.73 (1.87–3.17)
	Stage III (Developing)	21	1.24 (0.35–2.05)	130.50 (108.02–143.47)	3.67 (2.05–5.79)
	Stage IV (Maturing)	10	2.35 (0.71–5.86)	137.54 (128.21–144.58)	5.23 (2.66–7.82)
	Stage V (Mature)	7	7.15 (3.75–10.80)	131.52 (122.57–136.00)	8.04 (7.42–9.00)
	Stage VI (Gravid)	15	11.75 (5.40–27.50)	152.37 (118.00–191.00)	7.62 (5.00–12.00)
	Stage VII (Spent)	1	0.50 (–)	151.78 (–)	1.47 (–)
Males		177			
	Stage II (Immature)	98	0.42 (0.11–0.88)	134.31 (108.30–171.00)	2.34 (1.53–3.01)
	Stage III (Developing)	48	0.91 (0.40–1.78)	134.43 (112.35–142.64)	3.80 (3.20–5.05)
	Stage IV (Mature)	19	1.96 (0.55–9.11)	151.79 (122.12–209.00)	4.93 (3.44–7.58)
	Stage V (Spent)	12	0.27 (0.13–0.49)	136.76 (129.24–143.00)	1.92 (1.34–2.52)
Total		242			

This temporal pattern was robustly mirrored by trends observed in the gonadosomatic index. The cumulative population GSI exhibited significant seasonal variations (Mann-Whitney U test: U = 2841.5, p < 0.0001), registering minimum values during the dry season (February: 0.38 ± 0.06 SE, 95% CI [0.25, 0.51]; March: 0.49 ± 0.08 SE; May: 0.42 ± 0.07 SE). Conversely, prominent maximum peaks occurred during periods of intense rainfall, maximizing in June (1.75 ± 0.32 SE, 95% CI [1.06, 2.44]) and July (2.10 ± 0.41 SE, 95% CI [1.22, 2.98]). Significant differences in GSI were also confirmed across operational gonadal maturity stages for both females (Kruskal-Wallis test: H = 48.12, p < 0.0001) and males (H = 92.45, p < 0.0001), validating the physiological reliability of the macroscopic scale.

When segregated by sex, reproductive energetic allocation showed a severe dimorphism. Intersexual comparisons confirmed that female GSI values were significantly higher than male GSI values across the cycle (Mann-Whitney U test: U = 1820.0, p < 0.0001). Males maintained an extremely low, flat investment baseline throughout the cycle (varying narrowly between 0.23 ± 0.03 SE and 0.70 ± 0.11 SE). Conversely, female GSI values drove the overall population trends displaying profound seasonal spikes that maximized during the rainy months in June (7.53 ± 1.12 SE, 95% CI [4.80, 10.26]) and July (7.15 ± 0.98 SE, 95% CI [4.89, 9.41]).

Fecundity. Direct quantitative counts conducted strictly on gravid females (Stage VI; N = 15) indicated that absolute fecundity in *O. aenigmaticum* is relatively low but highly dependent on maternal bioenergetics. Absolute fecundity ranged from a minimum of 137 oocytes in a smaller female weighing 82.8 g to a maximum of 843 oocytes in the largest individual weighing 258.8 g, yielding a mean absolute fecundity of 353.86 ± 67.69 oocytes per female. A strong, directly proportional linear relationship was observed between absolute fecundity and total maternal body weight. In contrast, relative fecundity was highly variable and independent of body mass scaling, establishing a mean baseline reproductive output of 2.19 oocytes per gram of female body weight.

DISCUSSION

Demographic paradox and sex ratio asymmetries. The persistent dominance of male specimens observed in the evaluated population of *Ophisternon aenigmaticum* (overall ratio of 2.72:1) highlights a distinct demographic profile that deviates from the female-biased structures frequently documented in many Neotropical freshwater teleosts (Albert *et al*., 2020). Under contemporary evolutionary models for sex-changing teleosts, protogynous populations are theoretically expected to exhibit a female-biased structure dominated by smaller, younger individuals, with fewer, larger males derived from size-dependent sex inversion (Chong-Montenegro, Kindsvater, 2022). Therefore, the male-biased structure observed in Lake Catemaco presents an ecological paradox.

Although histological screening was not incorporated to track cellular germline transitions, the distinct asymmetric growth patterns observed in males (Stage IV), where paired structures fused into a single testicular mass, strongly align with macro-morphometric markers previously documented during sex reversal in synbranchids (Casas, Saborido-Rey, 2021).

To reconcile this demographic discrepancy, two alternative adaptive mechanisms must be considered. First, behavioral crypticism in females may heavily bias sampling efficiency; during active vitellogenesis, females frequently exhibit deep-burrowing behavior into the muddy substrate or dense root matrices to allocate energy to gonadal development and minimize predation risks, rendering them less vulnerable to capture than wide-ranging foraging males (Das, 2023). Second, localized environmental triggers and social structures in Lake Catemaco might disrupt classical size-structured transitions, accelerating protogynous shifts as a plastic reproductive tactic to optimize population fecundity under specific habitat constraints (Casas, Saborido-Rey, 2021). This structural demographic could indicate an accelerated transitional rate from females to males triggered by localized social cues or density-dependent mechanisms, representing a significant challenge to traditional understandings of reproductive plasticity in synbranchids.

Trophic specialization and ecomorphological adaptations. The extraordinary dominance of fish in the stomach contents of *O. aenigmaticum* (98.76%N) provides robust evidence of a highly specialized piscivorous behavior within the littoral environments of Lake Catemaco (Tab. 1). This finding strongly refutes the traditional paradigm characterizing Neotropical swamp eels as opportunistic generalists that primarily exploit benthic macroinvertebrates, insects, and detritus. In freshwater ecosystems, individual trophic niche variations and specific feeding behaviors are heavily shaped by both prey availability and the morpho-anatomical adaptations of the predator (Sánchez-Hernández *et al*., 2025).

From an ecomorphological standpoint, the complete evolutionary loss of paired fins, coupled with extreme body elongation, represents a highly derived morphospace configuration where elongation operates as the dominant axis of body shape evolution to exploit specific ecological niches (Camaiti *et al*., 2023). In the littoral zones of Lake Catemaco, particularly surrounding the dense, tangled root systems of Agaltepec Island, this finless anatomical design minimizes mechanical impediments and maximizes developmental and functional plasticity, allowing the species to successfully diversify its resource utilization within highly restricted physical matrices (Lofeu *et al*., 2021).

Unifying this locomotion-feeding integration, *O. aenigmaticum* functions as a highly specialized ambush predator, utilizing a low-energy stealth strategy where its body shape and gape characteristics optimize prey capture across shifting macro-seasonal variations (Luiz *et al*., 2026). This adaptation enables the species to navigate seamlessly through hyper-dense vegetative lattices, maintaining a constant regulatory pressure on native ichthyofauna and focusing its energetic demands almost exclusively on the continuous recruitment of the sympatric poeciliids *Poeciliopsis catemaco* and *Poecilia catemaconis* (Sabaj *et al*., 2022). The remarkable persistence of this piscivorous specialization across both seasons suggests that rather than shifting to alternative food items during environmental fluctuations, this species maintains a rigid trophic preference, leveraging the continuous multi-seasonal recruitment and high localized abundance characteristic of Neotropical poeciliids.

Reproductive seasonality and life-history trade-offs. The clear bimodal reproductive strategy displayed by *O. aenigmaticum*, characterized by synchronized

spawning windows during late autumn and mid-summer, reveals a tight evolutionary alignment with regional environmental dynamics. In Neotropical freshwater ecosystems, seasonal rainfall periods and shifting flood regimes act as critical macro-environmental triggers that orchestrate the reproductive investment and assemblage structure of fish communities (Costa *et al*., 2026). The dramatic energetic allocation observed in female specimens, evidenced by massive gonadosomatic index (GSI) spikes maximizing in June (GSI = 7.53) and November (GSI = 4.96), demonstrates that vitellogenesis is strategically timed to coincide with the onset of the heavy rainy seasons.

Mechanistically, these precipitation pulses induce rapid localized flooding along the littoral zones of Lake Catemaco, significantly expanding the availability of shallow macro-habitats and submerged marginal vegetation around Agaltepec Island. These temporary extensions of the aquatic ecosystem provide critical, nutrient-rich nursery zones and shelter from predators. By synchronizing maximum larval recruitment with these high-productivity rainy windows, *O. aenigmaticum* maximizes the survival and immediate foraging success of its early life stages, compensating for the energetic costs incurred by females during these profound seasonal metabolic shifts.

Finally, the trade-off observed between the relatively low absolute fecundity (353.86 ± 67.69 oocytes per female) and the remarkably large size of the vitellogenic telolecithal eggs (up to 4.5 mm in diameter) underscores a highly specialized life-history strategy. Within Neotropical aquatic lineages, the diversification of reproductive traits reflects a fundamental evolutionary divergence between high-fecundity opportunistic strategies and low-fecundity equilibrium strategies designed to maximize offspring survival in resource-limited or highly fluctuating microhabitats (Albert *et al*., 2020).

Producing large, yolk-rich spherical oocytes represents a significant maternal energetic investment that guarantees emerging larvae are born with substantial metabolic reserves and advanced initial sizes. In the dynamic lacustrine environments of Veracruz, where localized erosion, sedimentation, and seasonal hydrological variations impose severe physical stresses on benthic communities, these bioenergetic advantages are critical for ecological resilience (Silva *et al*., 2023). Larger, robust larvae possessing an immediate, superior capacity for executing active burrowing behaviors into the anoxic muddy substrates surrounding Agaltepec Island minimize early mortality rates caused by avian and piscine predation or physical displacement during heavy rainfall surges. This validates the evolutionary success of this low-fecundity, high-investment reproductive model in *O. aenigmaticum* at its northernmost distribution limit.

In summary, the results provide the first comprehensive baseline insights into the ecology and reproductive biology of *Ophisternon aenigmaticum* within Lake Catemaco, Veracruz, Mexico. Although the macro-morphometric characterization of gonads validated distinct developmental trajectories, the lack of germline histological analysis represents a formal limitation to definitively confirm active transitional phases or diandric pathways. Consequently, future research should incorporate detailed micro-anatomical gonadal histology across all size classes to complement this framework.

Nevertheless, the principal findings of this study demonstrate that the population maintains a persistent male-biased sex ratio across the cycle, a demographic profile likely shaped by sex-specific behavioral crypsis or accelerated transition rates. Furthermore, dietary abundance data conclusively refute the traditional opportunistic generalist paradigm for Neotropical swamp eels, revealing an extraordinary degree of

piscivorous specialization focused on the endemic poeciliids *Poeciliopsis catemaco* and *Poecilia catemaconis*. Combined with a bimodal reproductive seasonality synchronized with high-productivity rainfall periods and a low-fecundity equilibrium life-history model, these strategies reinforce the ecological resilience and evolutionary success of this specialized key benthic predator within Neotropical lacustrine ecosystems.

ACKNOWLEDGMENTS

NGR and OVM would like to thank the Instituto Politécnico Nacional (IPN), the Universidad Autónoma de Nuevo León (UANL), and the Instituto de Biología de la Universidad Nacional Autónoma de México (UNAM) for the institutional and logistical support provided during the development of this research, as well as for the use of their facilities.

REFERENCES

- **Albert JS, Tagliacollo VA, Dagosta F.** Diversification of Neotropical freshwater fishes. Annu Rev Ecol Evol Syst. 2020; 51:27–53. https://doi.org/10.1146/annurev-ecolsys-011620-031032
- **Camaiti M, Evans AR, Hipsley CA, Hutchinson MN, Meiri S, Anderson RO *et al*.** Macroecological and biogeographical patterns of limb reduction in the world's skinks. J Biogeogr. 2023; 50(2):428–40. https://doi.org/10.1111/jbi.14547
- **Casas L, Saborido-Rey F.** Environmental cues and mechanisms underpinning sex change in fish. Sex Dev. 2021; 15(1–3):108–21. https://doi.org/10.1159/000515274
- **Chong-Montenegro C, Kindsvater HK.** Demographic consequences of small-scale fisheries for two sex-changing groupers of the tropical Eastern Pacific. Front Ecol Evol. 2022; 10:850006. https://doi.org/10.3389/fevo.2022.850006
- **Costa JHA, Zuanon J, Selinger A, Souza UP, Duarte RM.** Drivers of fish beta diversity vary by habitat and rainfall period in temporary freshwater habitats of the Atlantic Forest. Front Freshw Sci. 2026; 4:1776529. https://doi.org/10.3389/ffwsc.2026.1776529
- **Das RK.** Taxonomy and conservation status of swamp eels (Synbranchiformes: *Synbranchidae*) of West Bengal, India. J Threat Taxa. 2023; 15(10):24032–42. https://doi.org/10.11609/jott.8595.15.10.24032-24042
- **Fricke R, Eschmeyer WN, Van der Laan R.** Eschmeyer's catalog of fishes: genera, species, references [Internet]. San Francisco: California Academy of Science; 2026. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp
- **Kang MG, Majeed S, Jung HK, Lee CI, Park HJ, Park JW *et al*.** Combined stomach content and stable isotope analyses revealed variations in trophic ecology of Pacific cod in the east sea. Sci Rep. 2025; 15:36339. https://doi.org/10.1038/s41598-025-20151-1
- **Lofeu L, Anelli V, Straker LC, Kohlsdorf T.** Developmental plasticity reveals hidden fish phenotypes and enables morphospace diversification. Evolution. 2021; 75(5):1170–88. https://doi.org/10.1111/evo.14221
- **Luiz OJ, Kopf RK, Olden JD, Crook DA, Kennard MJ, Saunders TM *et al*.** The functional effect of gape size on intraspecific body condition is variable across trophic groups and resource seasonality. Environ Biol Fishes. 2026; 109(41):1–14. https://doi.org/10.1007/s10641-026-01803-1

- **Mar-Silva AF, Arroyave J, Díaz-Jaimes P.** The complete mitochondrial genome of the Mexican-endemic cavefish *Ophisternon infernale* (Synbranchiformes, *Synbranchidae*): insights on patterns of selection and implications for synbranchiform phylogenetics. Zookeys. 2022; 1089:1–23. https://doi.org/10.3897/zookeys.1089.78182
- **Martín-Montero IE, Martínez-Vázquez JM, Perez IR, Torres M, Martos-Sitcha JA, Aguado-Giménez F.** Sex determination, evolution of gonadal stage in females, and seasonal evolution of sperm production in *Chelon labrosus* (Risso, 1827). Aquac J. 2024; 4(2):44–54. https://doi.org/10.3390/aquacj4020004
- **Muciño-Márquez RE, Echenique RO, Gárate-Lizárraga I, Figueroa-Torres MG, Esquivel-Herrera A.** Caracterización de la variación morfológica de *Cyanotetras* (Cyanobacteria) en el Lago de Catemaco Veracruz, México. Polibotanica. 2021; 1(51):43–53. https://doi.org/10.18387/polibotanica.51.3
- **Paschoal LRP, Zara FJ, Borges LEO, Azevedo-Santos VM.** Leucism in the marbled swamp eel *Synbranchus marmoratus* Bloch, 1795 (Synbranchiformes: Synbranchidae). Biota Neotrop. 2024; 24(3):e20231592. https://doi.org/10.1590/1676-0611-BN-2023-1592
- **Quispe-Salazar E, Sánchez J, Perea Á.** Classification models based on the gonadosomatic index to determine gonadal maturity stages: a case study in the Peruvian anchovy *Engraulis ringens*. Sci Mar. 2025; 89(4):e117. https://doi.org/10.3989/scimar.05636.117
- **Sabaj MH.** Codes for Natural History Collections in Ichthyology and Herpetology. Copeia. 2020; 108(3):593–669. https://doi.org/10.1643/ASIHCODONS2020
- **Sabaj MH, Arce H. M, Donahue D, Cramer A, Sousa LM.** *Synbranchus* of the Middle to Lower Xingu Basin, Brazil, with the description of a new rheophilic species, *S. royal* (Synbranchiformes: Synbranchidae). Proc Acad Nat Sci Phila. 2022; 166(1):1–23. https://doi.org/10.1635/053.166.0119
- **Sánchez-Hernández J, Larrea IF, Guzmán I, González JM, Larrañaga A.** Species-specific drivers explain fish feeding and individual niche variation. J Fish Biol. 2025; 107(4):1420–32. https://doi.org/10.1111/jfb.70136
- **Secretaría de Marina (SEMAR).** Derrotero meteorológico e histórico del Puerto de Catemaco, Veracruz [Internet]. Ciudad de México: Dirección General Adjunta de Oceanografía, Hidrografía y Meteorología; 2022. Available from: https://digaohm.semar.gob.mx/
- **Silva R, Martínez ML, Jiménez-Orocio O, Chávez V, Vázquez G, Cruz C *et al.*** La zona costera del municipio Catemaco, Veracruz. Veracruz: INECOL; 2023.

AUTHORS' CONTRIBUTION

Nayeli Gonzalez-Rodriguez: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Validation, Visualization, Writing-original draft, Writing-review and editing. **Osiris Valerio-Mendoza:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing-review and editing.

FUNDING INFORMATION

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors, and all activities were fully self-funded by the authors utilizing their own personal and laboratory resources.

ETHICAL STATEMENT

Experiments and biological procedures were formally approved by the Comité de Bioética Institucional de la Escuela Nacional de Ciencias Biológicas of the Instituto Politécnico Nacional (ENCB-IPN) under the official registration protocol code ZOO/02/11, adhering to the Mexican National Official Standard for the care and use of laboratory animals (NOM-062-ZOO-1999).

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author, OVM, upon reasonable request.

AI STATEMENT

The authors utilized the generative artificial intelligence model Gemini (Google) during the preparation of this manuscript. This AI-assisted technology was employed strictly for grammar correction to align with the journal's guidelines. The AI tool was not used for data collection, data analysis, core intellectual interpretation of the results, or the generation of scientific conclusions, for which the authors maintain sole responsibility and accountability.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary Material File

PEER REVIEW REPORT

Reviewers:

Anonymous reviewer #1

Anonymous reviewer #2

The peer review report is available at: Neotropical Ichthyology

HOW TO CITE THIS ARTICLE

- **Gonzalez-Rodriguez N, Valerio-Mendoza O.** Reproductive tactics and trophic ecology of *Ophisternon aenigmaticum* (Synbranchiformes: Synbranchidae) in a Neotropical Mexican lake. Neotrop Ichthyol. 2026; 24(4):e260097. https://doi.org/10.1590/1982-0224-2026-0097

Neotropical Ichthyology

OPEN ACCESS

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Distributed under
Creative Commons CC-BY 4.0

© 2026 The Authors.
Published by SBI

Official Journal of the
Sociedade Brasileira de Ictiologia

SBI