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RESEARCH PAPER

Reproductive traits of the European catfish, *Silurus glanis*, during the early stages of invasion

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Abstract. In recent decades, the European catfish *Silurus glanis* has spread across Europe and elsewhere, significantly impacting the native fauna of the recipient ecosystems. Studies on its reproductive traits from its non-native range are limited, although this is a critical step in developing effective management plans. Here, we explore the reproductive characteristics of invasive European catfish populations in the Lower River Tagus in Portugal, focusing on its sex ratio, size at maturity, spawning period, fecundity and oocyte diameter. European catfish were collected monthly by electrofishing, gill nets, baited hooks, and professional fishermen from January 2022 to November 2023. A total of 217 females, 156 males and 301 immature fish were analysed. The female-to-male sex ratio was 1.4 : 1, with females and males reaching size at first maturity (TL_{50}) at 72.9 and 68.8 cm total length, respectively. The spawning season was protracted, from February to June, showing asynchronous oocyte development patterns. The absolute fecundity was positively correlated with total length and total weight and ranged from 8,364 to 319,000 oocytes. Relative fecundity varied from 4.39 to 23.53 oocytes, with the mean diameter of the matured oocytes ranging from 1.50 to 3.21 mm. The results obtained in this study enhance our understanding of the reproductive biology of invasive species and can contribute to the development of effective management strategies, such as population control and density-dependent fecundity strategies.

Key words: Siluridae, size at maturity, gonadosomatic index, fecundity, oocyte diameter, asynchronous spawner

Introduction

Freshwater environments are among the most significantly impacted ecosystems by biological invasions (Reid et al. 2019), experiencing enormous biodiversity loss (Bellard et al. 2016), disruption of ecosystem services (Walsh et al. 2016) and substantial economic losses (Haubrock et al. 2022). Human-mediated activities drive these invasions through various species introduction pathways that operate at different spatial and geographic scales, like aquarium fish commerce, inland fisheries, maritime

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activity, aquaculture trade, and ornamental purposes (Tricarico 2012, Carpio et al. 2019). Fish intentionally introduced for economic or recreational purposes are released in locations where they are expected to thrive, with targeted introduction pathways prioritising species with desirable biological traits that favour their invasion success (Ruesink 2005). For example, certain species like salmonids and cyprinids to top predator fishes, exhibit biological traits beneficial for their survival and dominance in novel environments, which are favoured for sport fisheries introductions (Ribeiro et al. 2008, Carpio et al. 2019). This practice of introducing non-native gamefish is expected to persist, particularly in developed countries with a strong interest in angling. Because of this trend, it is crucial to implement management strategies that consider the life-history traits of the invasive species (Rahel & Smith 2018, Carpio et al. 2019).

Fish reproductive strategies are adapted to the environments in which they evolved. When introduced into non-native ranges, species may become invasive by surviving, reproducing, and expanding beyond their initial introduction points (Blackburn et al. 2011). While not all introductions lead to invasiveness, considerable life-history plasticity is commonly necessary for adaptation to new environments (Bøhn et al. 2004, Latorre et al. 2023). Reproductive success in a variety of environments strongly predicts invasiveness, especially when compared to species with specialised reproductive strategies (Olden et al. 2006). For instance, non-native freshwater fishes that are large, long-lived, early-maturing, and highly fecund often thrive due to extended lifespans that allow for higher growth and reproductive cycles, facilitating their spread (Vila-Gispert et al. 2005). For example, the invasive blue catfish *Ictalurus furcatus* in Virginia's Rivers James and York has demonstrated higher gonadosomatic indices than populations in their native range (Nepal & Fabrizio 2021). Similarly, the black bullhead *Ameirus melas*, when introduced to European rivers, exhibited a greater reproductive effort (higher relative fecundity) than populations in its native North American habitats (Copp et al. 2016). Thus, a thorough understanding of reproductive life history traits is critical for predicting and understanding species' potential to establish self-sustaining populations and succeed in non-native environments.

The European catfish, *Silurus glanis*, is among the tenth largest freshwater fish globally, reaching lengths up to 2.8 m and weighing 120 kg (Boulêtreau & Santoul 2016). It grows rapidly, achieving lengths of 1 m by age six and can live up to 70 years in the wild (Copp et al. 2009, Bergström et al. 2022). Its large size has made this invasive species a target for recreational anglers, leading to intentional introductions in western and southern Europe (Boulêtreau & Santoul 2016, Vejřík et al. 2019, Castagné et al. 2023) and countries like China, Tunisia, and Brazil (Cucherousset et al. 2018). The European catfish was first officially recorded in the Lower River Tagus (hereafter LRT, Portugal) in 2014, likely arriving in 2006 from Upper Tagus populations existing in Spain (Gkenas et al. 2015, Gago et al. 2016). Currently, the species thrives in the LRT and also in the River Douro, particularly in large reservoirs, with the invasion likely beginning with long-distance human-mediated introductions from Spanish populations, followed by short-range dispersal (Gago et al. 2016, Martelo et al. 2021, Santos et al. 2025). Portuguese populations of the European catfish have originated from the initial introduction in the Lower Ebro in 1974, as indicated by their high genetic resemblance (Castagné et al. 2023). It is found near submerged objects in higher-order rivers and exhibits tolerance to variations in water temperature, low levels of dissolved oxygen, high pollutant concentrations, and salinities up to 15 ppm (Carrasco et al. 2011, Huertas et al. 2016). Furthermore, the European catfish has a broader niche and more opportunistic diet than other predatory fishes (Vejřík et al. 2017), adapting to new resources and varying its diet seasonally and at different invasion stages (de Santis & Volta 2021). Invasive European catfish populations significantly impact ecosystems through competition and predation on native species, altering nutrient cycling and affecting overall ecosystem health (Vejřík et al. 2017, Cucherousset et al. 2018).

The European catfish has been extensively studied due to its significant ecological and economic impacts as a top predator in freshwater systems and its popularity as a recreational fishing target (Copp et al. 2009, Cucherousset et al. 2018, Vejřík et al. 2019). Despite numerous studies focusing on its predatory behaviour, research on its reproductive traits outside its native range remains limited (but see Panfili et al. 2024). Consequently, this study aims to examine the reproductive characteristics of the invasive European catfish population in the LRT approximately 15 years after its establishment. Our objectives are to: 1) establish the sex ratio, 2) estimate the size at first maturity (TL_{50}), 3) determine the spawning period, and 4) estimate fecundity. Furthermore, this research discusses these findings with available information on the reproductive biology of the European catfish from both its native and other invaded regions to better understand the ecological factors that facilitate

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successful invasions. The insights gained from this study are expected to significantly enhance invasive risk assessments and the development of effective management strategies.

Material and Methods

Study area and sampling

The Tagus is one of the largest rivers in the Iberian Peninsula, flowing 1,007 km from east-central Spain in the Sierra de Albarracín to the Atlantic Ocean near Lisbon, Portugal, draining an area of 80,600 km^2, of which 24,800 km^2 are within Portugal. The study was conducted in the lower part of the River Tagus Basin (39°4′19.17′′ N-39°40′3.32′′ N, 8°45′38.12′′ W-7°30′52.16′′ W) that includes a downstream part of 130 km of free-flowing waters where the river connects to the sea, preserving its longitudinal connectivity without noteworthy obstacles extending from the river mouth to the first hydroelectric structure – the Belver Dam. The climate is typically Mediterranean, with average monthly temperatures between 6 and 22 °C and an average annual precipitation of 750 mm yr^{-1} (SNIRH 2023). The hydrological regime has a strong seasonal and interannual variability, with high flows typically occurring in the winter, especially from November to February (495-650 m^3 s^{-1}) and low flows from June to September (140-187 m^3 s^{-1}) (SNIRH 2023). Mean monthly water temperatures in LRT vary between 11 °C in January and 23 °C in August, with temperatures never falling below 8 °C (see Santos et al. 2025). The LRT has been subjected to high anthropogenic pressure in the last decades, with impacts associated with land use changes (e.g. urbanisation, intensive agriculture) and urban and industrial pollution.

Samplings were conducted monthly from January 2022 to November 2023, encompassing two consecutive years (2022-2023) in the LRT, Portugal. Individuals of the European catfish (n = 674) were collected using electrofishing, gill nets, baited hooks, and from the catches of professional fishermen. Sampling of European catfish was suspended in December due to adverse winter conditions which posed significant challenges and safety risks to personnel. Monthly data on captured individuals were pooled after a preliminary analysis indicated no statistically significant differences between years (Kruskal-Wallis H, $\chi^2 = 0.97$, $P > 0.05$).

Laboratory processing and data analysis

European catfish were immediately iced upon capture and subsequently frozen for laboratory analyses. In the laboratory, fish individuals were thawed, and each fish was measured (total length – TL, 0.1 cm) and weighed (total and eviscerated weight – TW/EW, 0.01 g). Gonads were extracted to assess sex and maturity through gonadal analysis and were then weighed (gonad weight – GW, 0.001 g). Males with clearly distinguishable (white) testes were classified as mature. Females with ovaries containing non-yolked or indistinguishable eggs were classified as immature, and those with ovaries containing yolked eggs were classified as mature (Copp et al. 2016).

Female gonads from nine pre-spawning individuals, captured at the beginning of March and ranging between 79.1 and 92.9 cm TL, were fixed in 10% buffered formalin and subjected to histological preparations to assess the mean diameter of different oocyte stages. For each individual, a cross-section approximately 0.5 cm^3 from the middle of the right gonad was dehydrated in ethanol, embedded in methacrylate, sectioned at 3 µm, and stained with toluidine blue. Oogenesis stages were classified according to Wallace & Selman (1981). The thresholds for secondary growth (SG; cortical alveoli and early vitellogenic) and advanced vitellogenic (vitellogenic and mature) oocytes (hereafter, mature) were determined from the mean diameter of about 50 oocytes of each stage with a visible nucleus. The maximum and minimum diameters were used to minimise the error from the loss of spherical shape associated with histological processing. Measurements were made using the software package *ImageJ* (http://imagej.nih.gov/ij/).

The Chi-Square (χ^2) test was applied to overall and monthly sex compositions at a significance level of 0.05 to identify significant deviations from the expected 1 : 1 female-to-male ratio. Size at maturity (L_m) of both females and males was estimated following the logistic function: $P = 1/(1 + \exp[-r \times (TL - L_m)])$, where P – proportion of mature individuals in a length class, TL – fish total length, and r – model parameter (Zar 1996). The reproductive cycle and spawning period were derived from the gonadosomatic index (GSI) calculated as the percentage of gonadal weight of eviscerated weight GSI = 100 × (GW/EW). The GSI indicates gonad maturity, with higher GSI values suggesting more advanced gonadal maturation and lower values indicating less maturity (Nepal & Fabrizio 2021). To analyse monthly variations in the GSI of females and males, we applied nonparametric analysis of variance (Kruskal-Wallis tests), followed by multiple pairwise comparisons with the Wilcoxon rank sum (Zar 1996), as the data were non-normally distributed.

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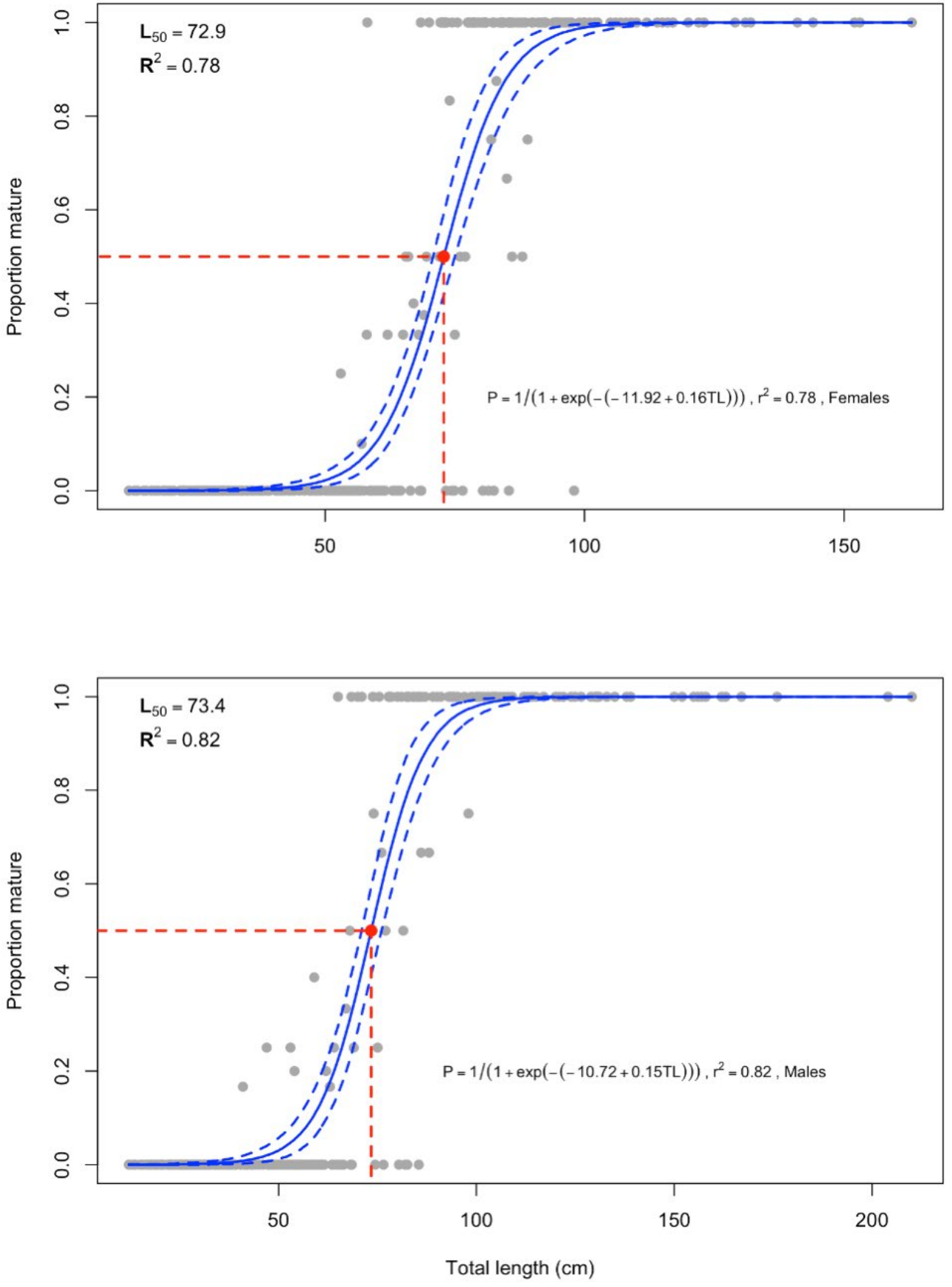

Fig. 1. Logistic regression curve of the proportion of mature female (upper panel) and male (lower panel) European catfish *Silurus glanis* specimens with total length in the Lower River Tagus (LRT). The solid line represents the model-predicted values, the dashed lines represent the corresponding 95% confidence intervals, and the red lines indicate the respective values in the Figure.

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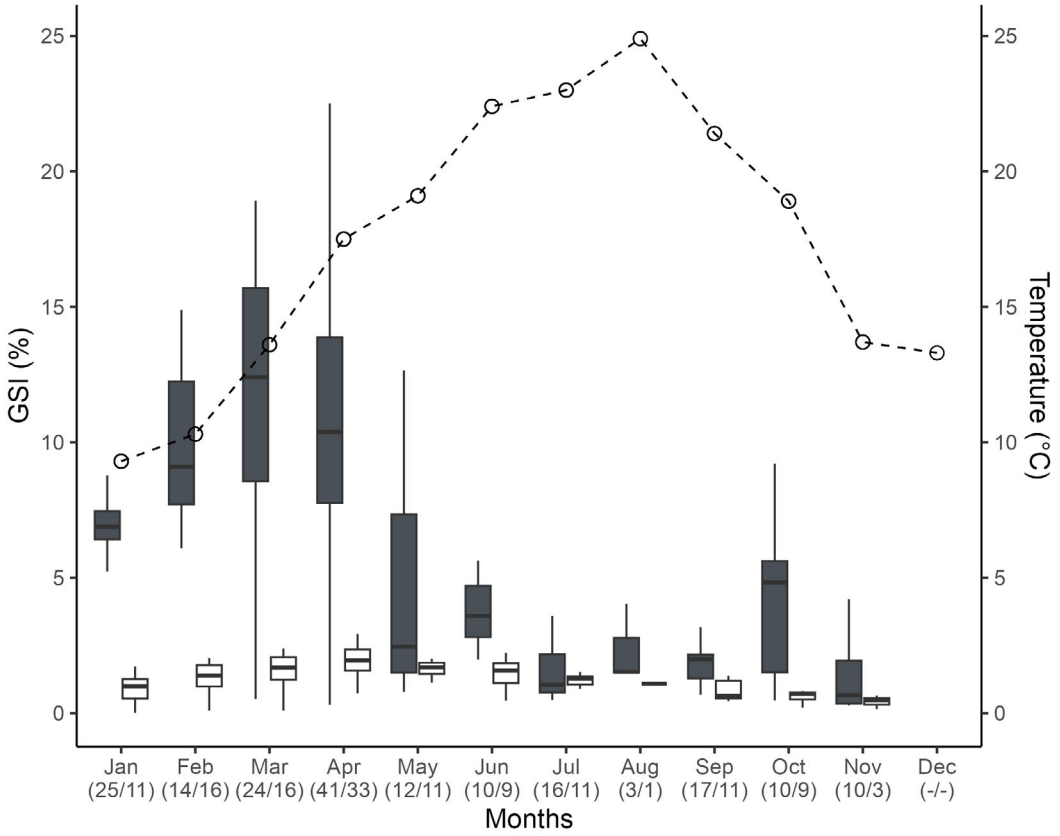

Fig. 2. Gonadosomatic-index (GSI) of female (dark colour) and male (white colour) European catfish *Silurus glanis* specimens in relation to water temperature (dashed line) in the Lower River Tagus (LRT). The box represents the interquartile range (IQR; 25th and 75th percentiles), and the line within the box is the median. Whiskers represent the 75th percentile + 1.5 × IQR and the 25th percentile + 1.5 × IQR. Water temperature values are shown as mean and extracted from the SNIRH database (https://snirh.apambiente.pt/). Numbers in brackets denote the number of female and male individuals used in the analysis, separated by a slash.

Fecundity was assessed in 63 mature females using the standard gravimetric method. Three subsamples (approximately 1 g) were randomly collected from the anterior, middle, and posterior sections of each gonad and weighed with a precision of 0.01 g, showing no significant variation in the number of oocytes among them ($\chi^2 = 1.17$, df = 2, $P > 0.05$). The absolute fecundity (AF) was estimated by counting the mature oocytes in each subsample and applying the formula: AF = (gonad weight × egg number in the subsample/gonad subsample weight) (Alp et al. 2004). Relative fecundity (RF) was calculated using the formula RF = AF/TW, dividing the absolute fecundity by the total weight of the fish. Oocyte diameter was measured for 30 randomly chosen mature oocytes from each of the anterior, middle, and posterior sections, totalling 90 oocytes, from 63 mature gonads using a stereoscope and *ImageJ*. Regression analyses were used to describe the relationship between fecundity and fish total length and body mass. Variations in fecundity and oocyte diameter across months were analysed with analysis of covariance (ANCOVA), with fish length as the covariate. To meet the assumptions of normality and homoscedasticity for absolute fecundity and oocyte diameter data, a log10 transformation was applied prior to analysis. All data processing and analyses were performed using R version 4.3.2 (R Development Core Team 2023).

A literature review was conducted on the reproductive traits of the European catfish across both its native and non-native habitats in Europe and Asia, including peer-reviewed and grey literature. A Boolean search was performed in Web of Science and Google Scholar using the operators AND, OR, and NEAR with different keyword combinations, including both common and scientific names of the species (e.g. *Silurus*, European catfish, wels catfish), terms indicating the origin of the species (e.g. native, non-native, invasive), and specific countries (e.g. Russia, Czech Republic, Turkey). The main focus of this review was to clarify the relationships among key reproductive traits, such as size at maturity, fecundity, and spawning period, and their patterns within the specified geographical regions. The diversity of data sources and the often incomplete information on sampling and laboratory methods

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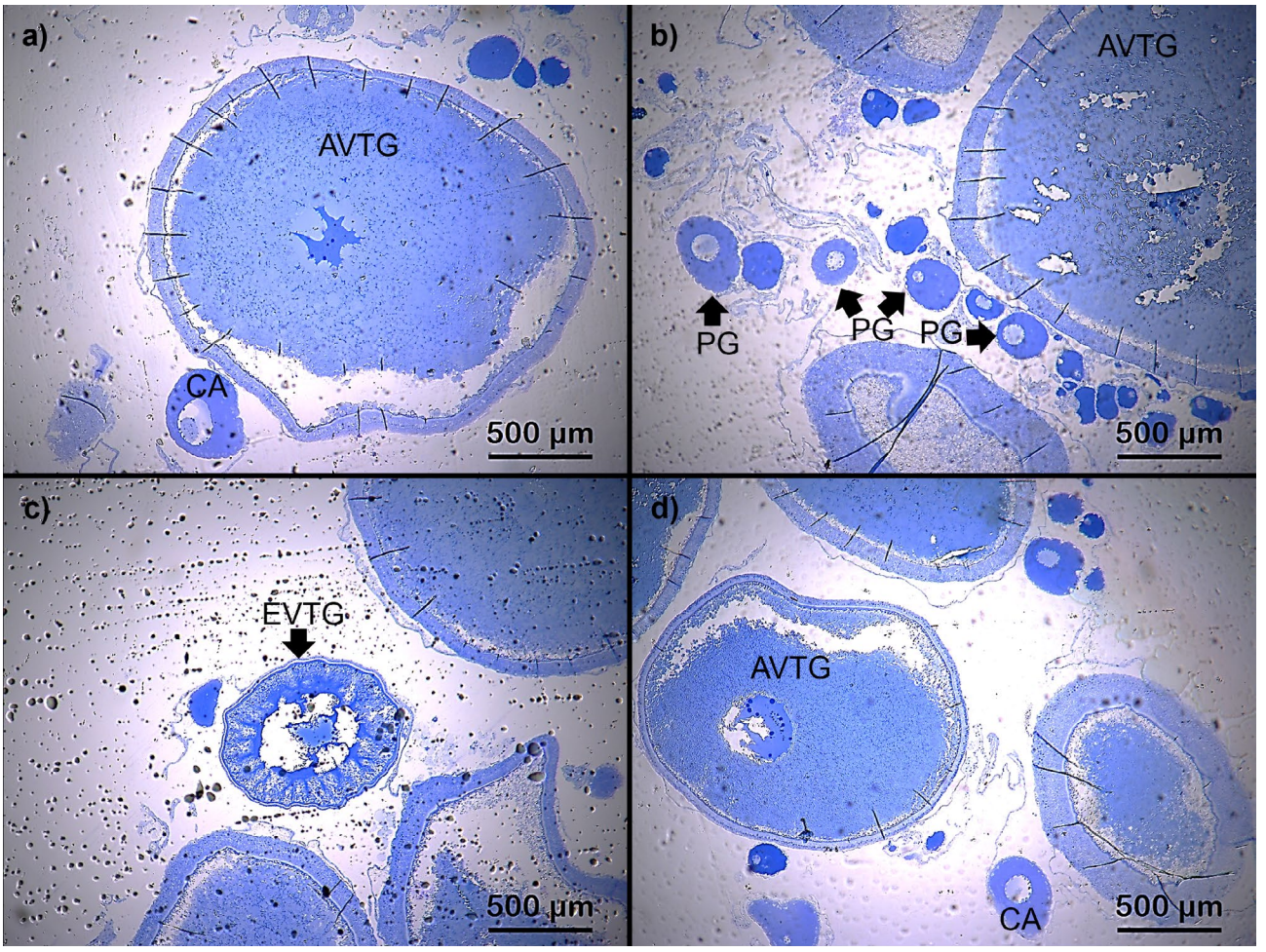

Fig. 3. Histological sections of reproductive active ovaries of European catfish *Silurus glanis*: a) ovary with CA and AVTG oocytes, b) ovary with several PG and AVTG oocytes, c) ovary with EVTG oocyte, d) oocyte with PG, CA and AVTG oocytes. AVTG – advanced vitellogenic oocyte, CA – cortical alveoli oocyte, EVTG – early vitellogenic oocyte, PG – primary growth oocyte.

used in the studies suggest that observed variations in the data may be due to differences in sampling or analytical methods.

During the preparation of this manuscript, we used ChatGPT (OpenAI 2024) to improve language clarity and readability. We declare that this tool was not used for data analysis, interpretation or creation of original text. The authors carefully reviewed and verified AI-assisted content to ensure accuracy and scientific integrity. This approach was adapted to align with ethical standards, promote transparency, and comply with the publication ethics of this Journal.

Results

A total of 674 individuals (217 females, 156 males and 301 immature) of the European catfish were collected from January 2022 to November 2023 in the LRT. The overall average total lengths were 85.23 cm ± 1.38 SE for females, 99.96 cm ± 2.29 SE for males, and 43.63 cm ± 1.02 SE for immatures (Table S1). The overall sex ratio was significantly female-biased, with a ratio of 1.4 females to 1.0 male ($\chi^2 = 9.65$, df = 1, $P = 0.002$) (Table S1). Monthly variations were evidenced, with female bias being greatest in January (2.3 females : 1 male, $\chi^2 = 4.69$, df = 1, $P = 0.030$) and September (2.1 females : 1 male, $\chi^2 = 7.45$, df = 1, $P = 0.006$). Both females and males reached 50% sexual maturity at similar sizes (Fig. 1). The smallest mature female recorded was 57 cm TL and the estimated size at 50% sexual maturity ($TL_{50\%}$) was 72.9 cm TL (95% CI = 70.8-75 cm TL), whereas the smallest mature male was 54 cm TL and the estimated size at 50% sexual maturity ($TL_{50\%}$) was 68.8 cm TL (95% CI = 66.5-71.7 cm TL) as determined by binomial regression.

GSI values for female European catfish were greater than males (Fig. 2). Significant variations in GSI values for females (Kruskal-Wallis H, $\chi^2 = 87.47$, $P < 0.001$) and males (Kruskal-Wallis H, $\chi^2 = 53.88$, $P < 0.001$) of European catfish were observed across sampling months. However, the GSI in males showed a weaker trend, with higher values

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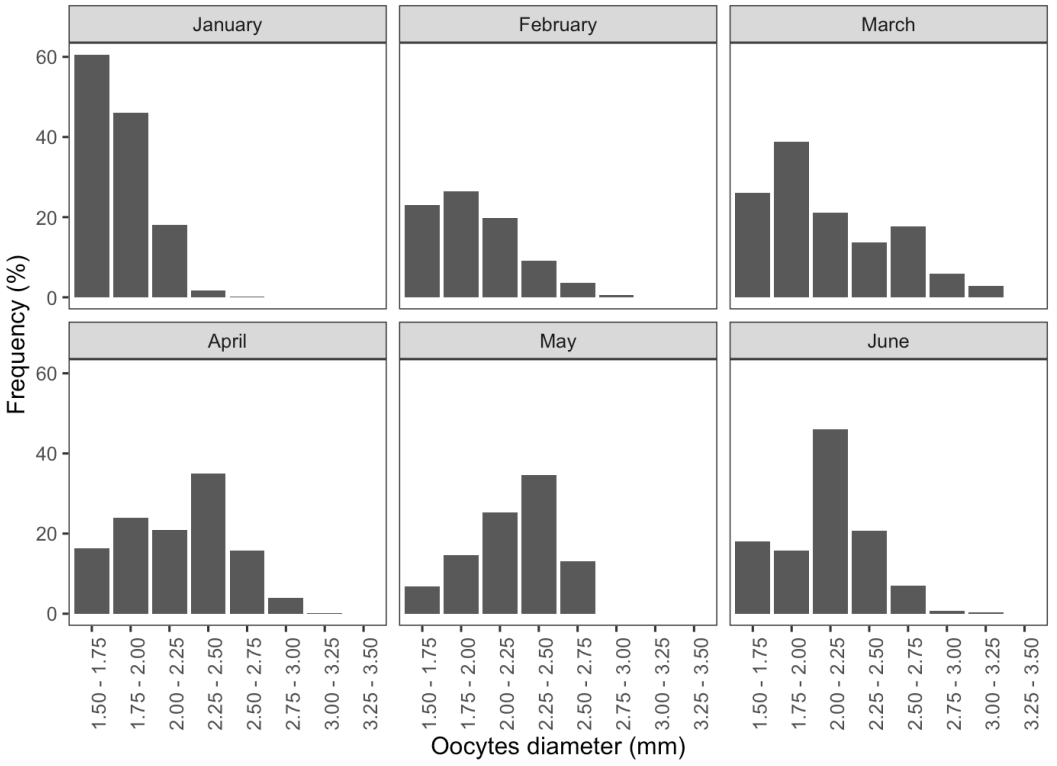

Fig. 4. Monthly size frequency distributions of oocyte diameter in ripened ovaries of European catfish *Silurus glanis* in the Lower River Tagus (LRT).

being recorded in April (1.87 ± 0.11 SE) and lower in November (0.43 ± 0.14 SE) (Fig. 2). For females, the reproduction cycle started in January when gonads began to develop (6.81 ± 0.32 SE). GSI values increased progressively in February (9.62 ± 1.00 SE), reaching a peak level in March (11.52 ± 1.12 SE) and remaining high in April (10.09 ± 0.89 SE) at mean water temperatures rising from 10.3 °C, to 13.6 °C, to 17.5 °C respectively (Fig. 2). Subsequently, GSI values declined sharply in May (4.42 ± 1.16 SE) when the mean water temperature was 19.1 °C. Female mean GSI values continued to decrease gradually, reaching their lowest levels in November (1.29 ± 0.41 SE). This pattern suggests that the spawning period of the European catfish extends from February to June, during which some females exhibited high GSI values (GSI max = 22.5%, Fig. 2). Additionally, elevated GSI values observed in some females in October may indicate sporadic reproductive activity or the start of maturation during the fall months.

Estimated oocyte mean diameter was 300 µm ± 77 SE for cortical alveoli (Figs. 3a, d), 597 µm ± 122 SE for early vitellogenic (Fig. 3c), and 1995 µm ± 309 SE for mature oocytes (Figs. 3a, b and c). Histological preparations from spawning females showed oocytes at different stages, suggesting an asynchronous development. The mean diameter of the matured oocytes ranged from 1.50 to 3.21 mm (mean = 2.05 ± 0.01 SE) and did not show significant differences among the anterior, middle, and posterior sections of the ovary (χ^2 = 0.01, df = 2, P > 0.05). Oocyte size-frequency distributions were continuous and asynchronous, with larger oocytes (1.75-2.25 mm) becoming more frequent in March and peaking at even larger sizes (2.25-2.75 mm) in April and May, likely signalling active spawning (Fig. 4). The oocyte diameter – fish length relationship varied significantly across months ($F_{5,4952}$ = 152.1, P < 0.001). The maximum average oocyte diameter was observed in May (2.22 mm ± 0.02 SE).

Absolute fecundity exhibited a wide range, varying from 8,364 to 319,000 oocytes per female, with a mean of 70,734 (± 7,561 SE). Relative fecundity showed variation from 4.39 to 23.53 oocytes per gram of TW, averaging 13.10 (± 0.54 SD). Absolute fecundity increased significantly with TL (ANCOVA, $F_{6,56}$ = 43.47, P < 0.001) and TW (ANCOVA, $F_{6,56}$ = 45.11, P < 0.001), supported by high R^2 values in the regression analyses for both TL and TW (Figs. 5a, b). In contrast, relative fecundity showed no significant relationships with either TL (P > 0.05, R^2 = 0.01) or TW (P > 0.05, R^2 = 0.01).

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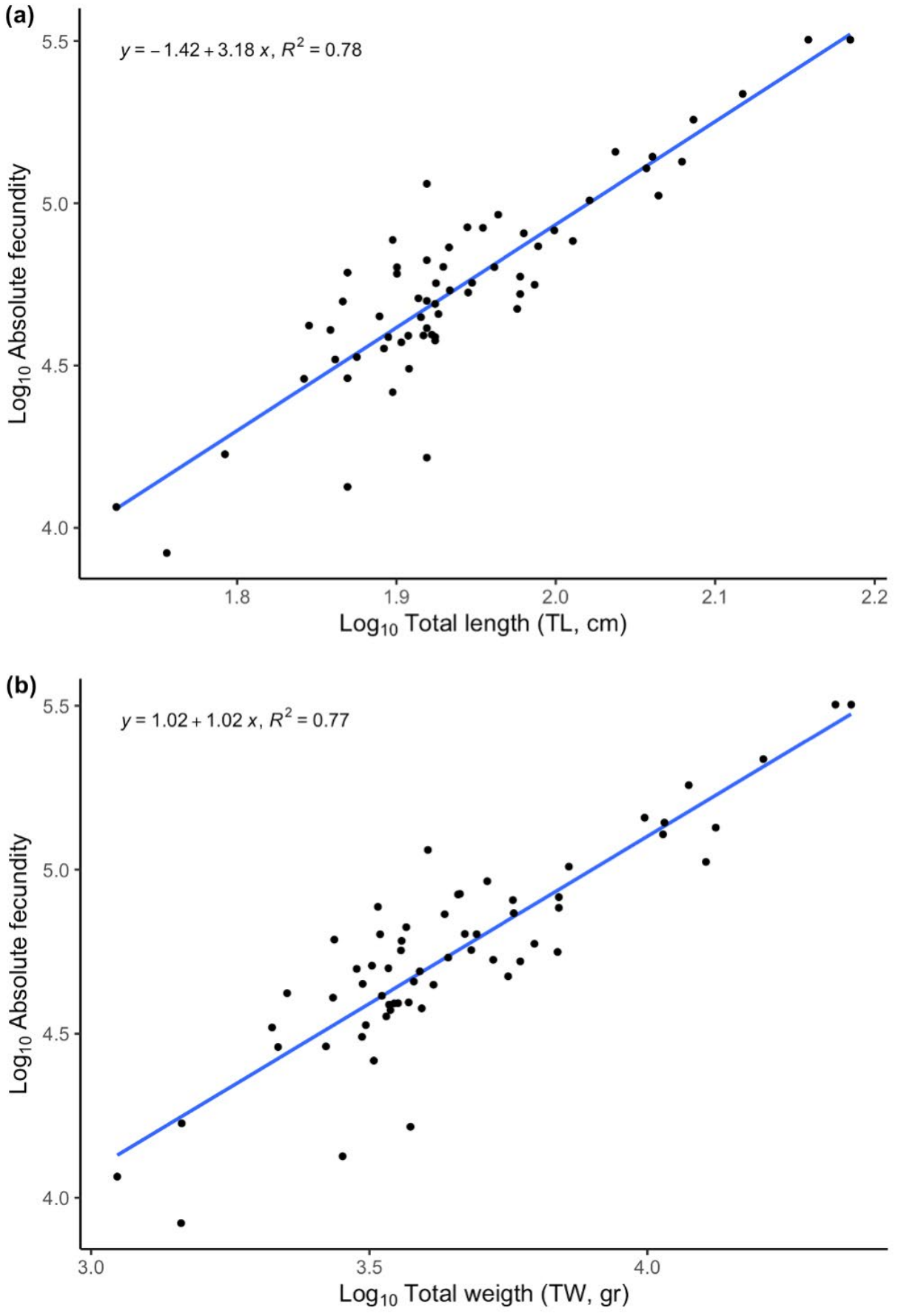

Fig. 5. Relationships between absolute fecundity and (a) total length (TL, cm) or (b) total weight (TW, gr) of female European catfish *Silurus glanis* in the Lower River Tagus (LRT).

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Table 1. Summary of reproductive traits of European catfish (*Silurus glanis*) obtained from a literature search of native and non-native populations, with reference to country, drainage, habitat type (delta, river, reservoir), origin (native, non-native), n – number of individuals analysed, TL – range of total length (cm), TW – range of total weight (g), GSI – gonadosomatic index in %, SP – spawning period observed in months, OD – mean oocyte diameter in mm, ROn – relative oocyte number per gram, Fec. Abs – absolute fecundity (nr. of oocytes), Fec. Rel. – relative fecundity (nr. of oocytes/kg of female weight), TL_{50} – total length at maturity of 50% of females (cm), with a respective reference number in the footnote.

Ecosystem (country)	Origin	n catfish ♀	TL (cm)	TW (kg)	GSI	SP	OD (mm)	ROn	Fec. Abs.	Fec. Rel.	TL_{50}
R. Volga[a] (Russia)	Native					mid May-mid July					60
R. Dnieper[a] (Ukraine)	Native		97-134	6.7-18		April-July			136,000-467,000		
R. Vistula & R. Bug[b] (Ukraine)	Native	15	127 84-175	17 4.2-36			1.34 0.25-2.50	571 243-1,114	339,306 34,700-788,000		
Kochowski Reservoir[c] (Ukraine)	Native	29		3.1-15.3				179-508	38,592-306,240		
R. Danube[d]	Native	80	68-236	2.5-76.0			2.7-3.0		11,810-1,380,000		
R. Dnieper[e] (Ukraine)	Native	15	55-132	1.4-22.0				135-499	27,400-384,500		
Orlik Reservoir[f] (Czech Republic)	Native		80-160	4.7-29.3				138-306	42,822-391,411		
R. Danube[g]	Native	1		12.7			3.0	198	356,400		
Waters of Dagestan[h] (Russia)	Native		42-193	1.2-41.3			2.0-3.0		14,600-285,000	29 7-42	
R. Vltava[i] (Czech Republic)	Native	11	88-129					130-730	61,400-249,300		
R. Volga[j] (Russia)	Native	252	55-266	1.3-114.0							
Khauzkhan Reservoir[k] (Turkmenistan)	Native		100-125	8.3-13.4			0.7-2.5		96,250-353,910	11.6-26.4	
Borçka Reservoir[l] (Turkey)	Native	99	20.6-135	0.06-15.8	0.1-3.5	July-September	1.1-2.6		179,043 30,379-301,356	20.2	85
R. Karasu[m] (Turkey)	Native					May-July	2.5			12.7	
Sıddıklı Reservoir[n] (Turkey)	Native	94			0.1-11.8	April-June	1.8 1.1-2.5		9,018-75,398	13.0 7.0-17.5	

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Table 1. continued

Ecosystem (country)	Origin	n catfish ♀	TL (cm)	TW (kg)	GSI	SP	OD (mm)	ROn	Fec. Abs.	Fec. Rel.	TL_{50}
Anzali Reservoir[o] (Iran)	Native	154			7.8	May-September					
R. Ticino[p] (Italy)	Non-Native	541			12	June-August			75,000 17,000-380,000	5.0-25.0	40-50 (55%)
Menzelet Reservoir[q] (Turkey)	Non-Native	135	33.4-135		4.6	June-August	2.1 1.0-3.7	195-800	9,033-340,461	8.4	87.1
Camargue Delta[r] (France)	Non-native				0.2-15.2	April-June			153,891 23,323-770,318	22.2 9.9-37.2	70.1
Tagus Basin[s] (Portugal)	Non-Native	217	57-163	1.2-30.0	6.7 0.3-22.5	February-June	2.1 1.5-3.2	153 62-257	70,734 8,364-319,000	13.1 4.4-23.5	72.9 70.8-75.0

[a]Berg (1949), [b]Wiśniewolski (1988), [c]Bielyj (1966), [d]Brujenko (1967), [e]Bugaj (1966), [f]Hochman (1967), [g]Ristić (1977), [h]Šichšabekov (1978), [i]Suchomelová (1952), [j]Kuzishchin et al. (2018), [k]Mukhamediyeva & Sal'nikov (1980), [l]Yesilcicek & Kalayci (2020), [m]Akyurt (1988), [n]Yazici et al. (2018), [o]Behmanesh et al. (2013), [p]Puzzi et al. (2003), [q]Alp et al. (2004), [r]Panfili et al. 2024 [s]Gkenas et al. (our study).

Discussion

The European catfish exhibits several biological traits, such as large body size, extended longevity, parental care, and high fecundity, which likely facilitated its invasion of Iberian freshwaters (Alcaraz et al. 2005, Ribeiro et al. 2008). While previous studies on the reproductive biology of this species were mainly conducted in native populations during the 20th century (Mukhamediyeva & Sal'nikov 1980, Orlova 1989, Copp et al. 2009), the current study represents one of the few comprehensive analyses of its reproductive characteristics within an invaded range, together with studies from Italy Puzzi et al. (2003), Turkey (Alp et al. 2004), and more recently, France (Panfili et al. 2024). Our results indicated that in the LRT, the European catfish exhibits an extended reproductive season, with active spawning occurring from February to June, achieving early maturity, showing high reproductive effort (GSI max = 22.5%), producing a large number of oocytes (8,364 to 319,000 oocytes), and having asynchronous oocyte development.

This study analysed a large number of females (n = 217), making it one of the most comprehensive analyses of European catfish reproductive biology. The primary spawning period in the LRT was from February to June, although a few unexpectedly high female GSI values were recorded in October. The mild Mediterranean climate of the region is likely to stimulate spawning activity by affecting the European catfish metabolic rates and hormonal patterns necessary for spawning (Copp et al. 2009, Panfili et al. 2024). In addition, this non-native habitat, characterised by warmer waters, low flows, and an abundant food supply from anadromous fish during winter and spring spawning migrations (Moncada 2024, Santos et al. 2025), may lead to advanced spawning of the European catfish. The lack of continuous histological analysis across different stages of oocyte development is a limitation of the study. However, the extensive GSI data and pre-spawning histological analysis from nine females provide valuable insights, indicating when European catfish are ready to spawn in March. These data may serve as a helpful indicator, allowing researchers to estimate the spawning season by correlating GSI changes with environmental factors such as water temperature. Although this approach does not provide a complete picture, our analysis offers essential observations into the reproductive status of the European catfish females, confirming the maturity state and readiness for reproduction of the

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species, thus contributing to the understanding of critical reproductive dynamics.

In this study, an overall female-biased sex ratio of 1.4 : 1.0 was found. Behavioural differences between females and males could explain the higher dominance of females in our samples. For instance, males might be less mobile during the spawning season as they guard their nests (Copp et al. 2009), making them less likely to be captured by gill nets (F. Ribeiro, pers. observ.). The sex ratio in our study is consistent with findings from European catfish populations at the Borçka Dam (Yesilcicek & Kalayci 2020), yet contradicts observations from other studies (Alp et al. 2004, Yazici et al. 2018). Consequently, these differences could relate to habitat characteristics, sampling periods, fishing gears and movement patterns (Santos et al. 2025), potentially biasing the sex ratios.

Our results indicated that the size at first maturity of the European catfish differed between sexes, with females reaching maturity at a larger size (TL_{50} = 72.9 cm) than males (TL_{50} = 68.8 cm). This size at maturity in the LRT is smaller than that observed in Turkey, both in non-native (Menzelet Reservoir) and native (Borçka Reservoir) populations, with females maturing at around 87 cm TL and males at 79 cm TL (Alp et al. 2004, Yesilcicek & Kalayci 2020). However, Panfili et al. (2024) reported a similar TL_{50} for females at 70.1 cm but a smaller one for males at 54.1 cm in the Camargue Delta (Southern France), where it is non-native (Table 1). Earlier studies have also shown great plasticity in size at first maturity among different native Central European and Western Asian catfish populations. For instance, in Orlik and Khauzkhan reservoirs and in the River Volga, European catfish started to mature at sizes ranging between 57 and 71 cm (Hochman 1967, Mukhamediyeva & Sal'nikov 1980, Orlova 1989). Additionally, a previous study in the River Po revealed that 55% of females in non-native ranges matured at even smaller sizes (40-50 cm TL) (Puzzi et al. 2003) (Table 1). These variations in the TL_{50} among European catfish populations are likely influenced by local factors, such as habitat conditions, temperature, food availability, and growth rate (Copp et al. 2009, Yesilcicek & Kalayci 2020).

The spawning period of the European catfish in the LRT extended from February to June, coinciding with water temperatures between 11 °C and 23 °C, and was marked by both the longest duration and the highest mean GSI values ever published in the literature (Copp et al. 2009, Panfili et al. 2024). These findings are consistent with observations from native European catfish populations in the Borçka and the Sıddıklı Reservoirs (Turkey), which reproduce from April to June at water temperatures of 14.9 °C to 20.8 °C (Akyurt 1988, Yazici et al. 2018, Yesilcicek & Kalayci 2020), with maximum GSI values ranging from 3.5% to 11.8%. Similarly, non-native populations in France reproduce between April and June at water temperatures of 18-20 °C and peak mean GSI values of 8.1 (Panfili et al. 2024) (Table 1). In colder climates, in Eastern Europe, spawning occurred from April to July in the Dnieper Delta and from mid-May to mid-July in the Volga Delta (Berg 1949) (Table 1), coinciding with water temperatures of 18-22 °C (Copp et al. 2009). However, even later spawning periods have been recorded for non-native European catfish populations, ranging from June to August in the Menzelet Reservoir (Alp et al. 2004) and from July to August in the River Po (Puzzi et al. 2003), with GSI values ranging from 5% to 12% (Table 1). Since the invaded ranges of the European catfish are often highly modified water bodies (Cucherousset et al. 2018), like the LRT in this study, the species likely benefits from the prevailing environmental conditions. As European catfish display high predation on migratory fish species (shads, mullets, European eel), native fish (barbels) and crustaceans (crayfish, shrimps) throughout the year (Ferreira et al. 2019, Moncada 2024), this behaviour may explain the increased energy allocation towards reproduction and the highest GSI in the studied invaded area (Panfili et al. 2024).

Absolute fecundity increased with length and mass, following expected patterns in fish (Winemiller & Rose 1992). Similar positive relationships between fecundity and total length or weight have been documented in European catfish populations across both native (Akyurt 1988, Yazici et al. 2018, Yesilcicek & Kalayci 2020) and non-native regions (Puzzi et al. 2003, Alp et al. 2004, Panfili et al. 2024). In our study, the European catfish exhibited high fecundity, with values ranging from 8,364 to 319,000 oocytes, consistent with previous studies that ranged from 9,033 to 380,000 oocytes (Puzzi et al. 2003, Yazici et al. 2018, Yesilcicek & Kalayci 2020) (Table 1). However, our estimates were lower than those reported from the Camargue region (Panfili et al. 2024), River Vistula (Wiśniewolski 1988) and Danube (Brujenko 1967), where fecundity varied widely from 770,318 to 1,380,000 oocytes, respectively (Table 1). We recorded a mean relative fecundity of 13.1 oocytes per gram (4.4-23.5 oocytes per gram), comparable to other Turkish populations (8.4-20.2 oocytes per gram,

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Akyurt 1998, Yazici et al. 2018, Yesilcicek & Kalayci 2020) but lower than French (22.2 oocytes per gram, Panfili et al. 2024) and Eastern European populations (29.0 oocytes per gram, Šichšabekov 1978) (Table 1). The different findings may be attributed to a range of methodological approaches, including the processing of gonads and selection criteria for oocyte classification for fecundity determination, which in our case study was more conservative, as we only considered matured oocytes with an oocyte diameter larger than 1.50 mm.

In this study, we observed that the diameter of mature oocytes of the European catfish ranged from 1.50 to 3.21 mm with an average diameter of 2.05 mm, comparable with findings from its native (Akyurt 1988, Wiśniewolski 1988, Yazici et al. 2018) and non-native ranges (Alp et al. 2004) where mean oocyte diameters of different stages ranged from 1.30 to 2.50 mm (Table 1). Additionally, our analysis revealed a significant positive correlation between oocyte size and both fish length and sampling months, indicating that larger females tend to produce larger oocytes, as observed previously (Alp et al. 2004, Yazici et al. 2018, Yesilcicek & Kalayci 2020). Furthermore, histological analysis of gonads revealed different stages of oocytes coexisting within individual females, suggesting that the European catfish is an asynchronous spawner. This asynchronous development of oocytes, a common reproductive strategy among freshwater catfish, allows females to spawn multiple batches of oocytes over time (Moyle 2002, Copp et al. 2016, Nepal & Fabrizio 2021). Such a strategy ensures that at least some oocytes will survive and hatch in unpredictable environments and permits adjustments in the size and number of oocytes produced in response to local environmental conditions.

Management of the invasive European catfish is challenging, and specific actions should be context-dependent, considering the species' popularity among anglers and the legal framework (Banha et al. 2024). The current legal framework in Portugal mandates that this invasive fish should not be released after capture, imposes no limit on the number or catch size, and permits fishing without seasonal restrictions (National List of Invasive Species, Annex II, Law Decree Nr. 92/2019). This study provides crucial data for implementing informed population control actions to enhance their effectiveness. Size at first maturity is a critical parameter for targeting individuals with reproductive capability, and thus all adult fish should be targeted for removal. Increasing fishing efforts during the spawning period from February to June will exploit the catfish's vulnerability when they aggregate in specific areas (Santos et al. 2025), thereby increasing removal efficiency. Notably, the European catfish activity patterns peak after April, potentially increasing capturability, especially with passive standard fishing gear such as gill nets (Santos et al. 2025). Additionally, a significant positive correlation between fecundity and body size supports the selective removal of larger individuals, given that these individuals have a greater reproductive output, thereby influencing disproportionately its recruitment. This outcome could be achieved using baited longlines that capture larger individuals (Vejřík et al. 2024) rather than gill nets (F. Ribeiro, pers. observ.). However, we need to consider the impact of density-dependent strategies on fecundity, particularly when larger individuals of European catfish are targeted for removal. Removing these individuals may increase resources per capita, leading to compensatory fecundity where younger, smaller individuals may increase their reproductive effort due to reduced competition. To prevent such compensatory effects, management strategies must be adjusted based on continuous monitoring of population dynamics and reproductive rates to maintain an optimal density that supports ecological balance (Melero et al. 2015). Consequently, our management tactics in the LRT should focus on: 1) promoting fishing across all adult fish to reduce species reproductive success, particularly targeting large females, 2) amplifying removal efforts during spawning to leverage fish aggregations (see Santos et al. 2025), 3) improving removal techniques with longlines or gill nets (Vejřík et al. 2024), and 4) establishing a monitoring program to assess impacts on both the invasive population and the broader ecosystem (de Santis et al. 2024).

Conclusions

To summarise, the European catfish exhibits reproductive traits associated with a female-biased sex ratio, early maturity, long spawning season, high fecundity, and asynchronous development. Evidence suggests that the European catfish in LRT may have benefited from the high water temperatures and diet resources in the LRT, which enable the species to remain active and display high levels of reproductive traits plasticity, similar to observations made by Panfili et al. (2024) and for other catfish species in invaded areas (Copp et al. 2016, Nepal & Fabrizio 2021). Additionally, the role of the European catfish as an apex predator (Vejřík et al. 2017) contributes to its establishment and may result in its predominance

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in the LRT, as observed in other Mediterranean ecosystems (Castaldelli et al. 2013, Almeida et al. 2017, Panfili et al. 2024). This predominance could cause the reduction or extinction of native fish populations, including some imperilled endemic species in the River Tagus (Mateus et al. 2013, Veríssimo et al. 2018, Magalhães et al. 2023).

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Author Contributions

C. Gkenas: conceptualisation, data analysis and visualisation, writing – original draft; V. Sequeira: methodology, laboratory process, writing – review and editing; D. Ribeiro: methodology, laboratory process, writing – review and editing; J. Gago: methodology, laboratory process, writing – review and editing; D. Dias: methodology, laboratory process, writing – review and editing; C. Verma: methodology, laboratory process, writing – review and editing; P. Kumkar: methodology, laboratory process, writing – review and editing; F. Ribeiro: investigation, conceptualisation, resources, writing – review and editing. All authors read and approved the final manuscript.

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Supplementary online material

Table S1. Numbers of female, male and immature European catfish Silurus glanis collected in the Lower River Tagus (LRT) and monthly comparisons of sex ratio using $\chi 2$ (https://www.ivb.cz/wp-content/uploads/JVB-vol.-74-2025-Gkenas-Ch.-et-al.-Table-S1.pdf).

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