






Equilibrium reproductive strategy of the peacock bass *Cichla kelberi* facilitates invasion into a Neotropical reservoir

Gustavo Henrique Soares Guedes¹  | Iracema David Gomes¹  |
 Aparecida Alves do Nascimento²  | Fernanda Silva de Aguiar¹  |
 Francisco Gerson Araújo¹ 

¹Departamento de Biologia Animal, Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil

²Departamento de Biologia Animal, Laboratório de Histologia e Embriologia Animal, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil

Correspondence

Francisco Gerson Araújo, Departamento de Biologia Animal, Laboratório de Ecologia de Peixes, Universidade Federal Rural do Rio de Janeiro, Km 7, BR-465, 23.890-000 Seropédica, RJ, Brazil.
 Email: gerson@ufrjr.br

Funding information

Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro, Grant/Award Number: E-26/201.248/2014; LIGHT ENERGIA S. A, Grant/Award Number: 4600004989

Abstract

The reproductive strategy of the non-native predator cichlid *Cichla kelberi* was determined to explain its success after more than 60 years of being introduced into an isolated reservoir in southeastern Brazil. This was one of the first-known translocations of the genus *Cichla* out of its natural range. Macro- and microscopy characteristics of the gonadal development stages and the maturation phases, along with the reproductive features (size at first maturation size, gonado-somatic index and sex ratio), were described. It was hypothesized that the stable conditions of the reservoir, with low connectivity, weakly defined spatial gradient and slight seasonal changes in environmental variables, favour the equilibrium strategy that enables predators to have high offspring survivorship because of great parental investment in individual progeny. Sex ratio was well balanced, with males and females reaching first maturity between 30.0 and 28.6 cm total length (L_T), respectively. The stages of oocyte (primary and secondary growth, vitellogenic and atresia) and spermatocyte (spermatogonia, spermatocytes, spermatids and spermatozoa) development were identified. Five phases of gonadal development (immature, developing, spawning capable, regressing and regenerating) were described for both sexes. A long reproductive season was found, with spawning peaks in August/September and, to a lesser extent, in April/May. Parental care and spawns in parcels (batch spawns) corroborated the raised equilibrium strategy that was effective in this isolated reservoir. This species developed reproductive mechanisms that fit to different environmental conditions, with multiple spawning being associated with lentic environments and asynchronous development of oocytes, which are released over long periods. The reproductive plasticity in reservoirs may be one of the main factors inherent to the successful of colonization and establishment of the peacock bass in the environments in which they were introduced.

KEYWORDS

Cichlidae, gonadal development, histology, reproductive plasticity

1 | INTRODUCTION

The ichthyofauna of the Neotropical region is the most diverse on Earth, with remarkable variation in morphology, habitats, physiology, behaviour and life history (Reis *et al.*, 2016). Although fish reproductive traits vary considerably, three general strategies (periodic, opportunistic and equilibrium) are recognized, which reflect trade-offs among the basic demographic parameters of survival, fecundity and duration of reproduction (Winemiller, 1989; Winemiller & Rose, 1992). Man-made environmental changes in recent centuries, such as the fragmentation of rivers by dams, posed challenges to which fish are not naturally adapted (Poff *et al.*, 1997). Species with periodic strategy, *e.g.*, indicated by large body size, late maturation, high fecundity and low offspring survivorship, are likely to be favoured in highly periodic (seasonal) environmental conditions, many of them reophilic and long-distance migrators, and are the most impacted by river fragmentation. Opportunistic strategists (small-bodied species with early maturation and low offspring survivorship) are favoured in environments with frequent and intense disturbances (Winemiller & Rose, 1992). The species with equilibrium strategy (small-to-medium body size, low fecundity per spawning event and high offspring survivorship mainly because of high parental care) can take advantage of river fragmentation by dams due to flow regulation, the creation of lentic zones and greater water stability, which are advantageous in nest building and offspring protection (Mims & Olden, 2012). Therefore, fragmentation of rivers by dams can influence a whole set of characteristics of fish life history, especially those related with reproduction (Agostinho *et al.*, 2004).

Fish of the genus *Cichla* Bloch & Schneider, 1801, are among the main top predators of the family Cichlidae in Neotropical river basins (Kullander & Ferreira, 2006; Willis *et al.*, 2007; Winemiller *et al.*, 1997). Attributes such as meat quality, lush colours, control of forage species and value to sport anglers have led to *Cichla* species being widely translocated to South America and introduced in various regions of the globe, such as Central America (*e.g.*, Sharpe *et al.*, 2017), North America (Shafland, 1999), Asia (Chong *et al.*, 2010), Africa (Welcomme, 1988), Oceania (Maciolek, 1984) and, most recently, the Middle East (Golani *et al.*, 2019). A main concern is that *Cichla* spp. easily settled in the new environments in which they were introduced, causing severe impacts on the native communities, including changes in the food web, reduction in prey stocks and local extinctions (*e.g.*, Menezes *et al.*, 2012; Pelicice & Agostinho, 2009; Sharpe *et al.*, 2017). Therefore, it is important to know the characteristics of life history, such as how the reproductive aspects determine how species establish self-sustaining populations outside their native range of distribution, as well as try to predict the likely impacts of invasion.

Many aspects of *Cichla* spp. reproduction have been extensively studied (*e.g.*, Jepsen *et al.*, 1999; Muñoz *et al.*, 2006; Winemiller *et al.*, 1997). The etymological origin of the word “Tucunaré,” the popular name of the species of the genus *Cichla* in Brazil, provides a first clue about the reproduction of these species. “Tucunaré” is a word derived from the Tupi-Guarani indigenous language and is formed by

the prefix “Tucun,” meaning “tree” (Amazonian palm), and “aré,” meaning “friend,” which can be translated into “friend of tree” (Dictionary Tupi-Guarani, 2019). The affinity of these cichlids for trees may be associated with their reproductive behaviour, as the peacock bass build nests and lay their adhesive eggs preferentially on submerged branches (Muñoz *et al.*, 2006). Both sexes of *Cichla* exhibit parental care, and during the spawning period, males have secondary sexual characteristics, observed by Darwin (1889, p. 340): “I hear from Professor Agassiz, that mature males have a conspicuous protuberance on the forehead, which is wholly wanting in the females and in the young males.” Professor Agassiz adds, “I have often observed these fishes at the time of spawning when the protuberance is largest, and at other seasons when it is totally wanting, and the two sexes show no difference whatever in the outline of the profile of the head. I never could ascertain that it subserves any special function, and the Indians on the Amazon know nothing about its use.” These protuberances resemble, in their periodical appearance, the fleshy caruncles on the heads of certain birds; but whether they serve as ornaments must remain at present doubtful (Chellappa *et al.*, 2003).” In addition to the possible ornamental function cited by Darwin (1889), the post-occipital protuberance is formed by an accumulation of adipose tissue and, unlike birds, can function as a lipid allocation to be used in the period of parental care.

Aspects of the history of the peacock bass, such as sedentary local populations, prolonged breeding seasons and parental care, are associated with an equilibrium strategy (Winemiller, 1989). Empirical evidence suggests that equilibrium strategies are also related to more stable environments, with less hydrological variability and increasing stability (Mims & Olden, 2012). Nevertheless, the very global spread of *Cichla* indicates that these populations are subjected to contrasting climatic and hydrological conditions. Invasiveness capability seems not to be influenced by genetic diversity and hybridization (Carvalho *et al.*, 2014). Persistence in new environments seems to be linked to phenotypic plasticity in reproductive traits such as fecundity (Normando *et al.*, 2009), size at first maturation (Chellappa *et al.*, 2003; Gomiero *et al.*, 2009) and spawning season (Jepsen *et al.*, 1999; Marto *et al.*, 2015; Vieira *et al.*, 2009). The variability in reproductive traits shown between different populations of *Cichla* demands that accurate local information be generated to support the correct management of these species, which are today one of the principal invasive piscivores in the world.

This study evaluated whether an equilibrium strategy (*sensu* Winemiller, 1989) and reproductive aspects such as gonadal histology, sex ratio, reproductive period, size at first maturation and other biological features could have facilitated the establishment of *Cichla kelberi* Kullander & Ferreira, 2006, in the Lajes Reservoir, southeastern Brazil. This species was introduced into this reservoir in the 1950s to control forage fish overpopulation and to improve local angling, one of the first-known translocations of the genus *Cichla* out of its natural range. It is hypothesized that the stable conditions of the Lajes Reservoir, an isolated reservoir, with low connectivity, weakly defined spatial gradient and slight environmental changes, favour the equilibrium strategy that enables non-native predators to colonize stable environments.

2 | MATERIALS AND METHODS

2.1 | Study area

Lajes Reservoir (22° 42' N–43° 53' W, 22° 50' N–44° 05' W) is a 30 km² impoundment, located 415 m a.s.l. in Rio de Janeiro State, in southeastern Brazil (Figure 1). This reservoir was filled between 1905 and 1908 mainly for hydroelectric purposes (Araújo & Santos, 2001). It is located in the upper slopes of the Serra do Mar (Sea Mountains) in the East Hydrographic Basin and off the main channel of a medium or large river with its outflowing and discharged waters draining into the Guandu River basin.

The water balance is mainly regulated by the transposition of water from an adjacent watershed and the contribution of small streams, by the seasonal rainfall with peaks in January–February (149.9 mm per month) and by the controlled discharges of the hydroelectric power plant. The mean inflow of water is 13.7 m³ s⁻¹, of which most of the flow (8.3 m³ s⁻¹) is received by transposition from the interbasin diversion (Guedes *et al.*, 2020). As a consequence, extreme differences in the water level annual fluctuation can reach up 12 m (mean ≈3 m), ranging from lowest values in October–November (409.4 ± 0.1 m a.s.l.) to the highest in May–June (412.4 m a.s.l.) (Araújo & Santos, 2001; Santos *et al.*, 2004). Thus, anthropogenic management in the reservoir causes the highest water levels to occur in the period with low rainfall.

The water retention time (≈300 days) and water transparency (euphotic zone = 9.2 m) are high, and oligo-mesotrophic conditions predominate (Guarino *et al.*, 2005; Soares *et al.*, 2008). Lentic conditions predominate in the longitudinal extent of the reservoir because of the low connectivity with tributaries and the dendritic reservoir morphology (Guedes *et al.*, 2020). The climate is seasonal tropical with dry winters (Aw), according to the Köppen–Geiger classification.

2.2 | Data collection

Fish specimens and environmental variables were collected monthly between August 2015 and July 2016 as part of the faunal survey. Water temperature (°C) was measured using a U-52 G multiprobe (Horiba, 192 Ltd., Kyoto, Japan). Water transparency (cm) was obtained with a Secchi Disk. Monthly rainfall (mm) and water level (m a.s.l.) data were obtained from the local hydrometeorological station (V-3-485) and provided by the hydroelectric company Light Energia S.A. Averages and standard deviations of the environmental variables are shown in Supporting Information Figure S1.

The collections were performed using monofilament gillnets (20 × 50 × 2 m; 25–55 mm stretched knots mesh-size) set at the banks at dusk and collected at dawn after a period of c. 12 h. After collection, fish were anaesthetized in benzocaine hydrochloride (50 mg l⁻¹) and then killed by immersion in water at 4°C. In the laboratory, fish were identified, measured to total length (L_T , ±0.1 cm) and weighed to total body mass (M_T , ±0.1 g). The care and use of experimental animals complied with the ICMBio, the Brazilian Environmental Agency, animal welfare laws (Brazilian Federal Law 11.794 of 8 October 2008), guidelines and policies as approved by the Ethics Council of Animal Use (CEUA/ICBS/UFRRJ) through permission number 12179.

Gonads were extracted and weighed (M_G , ±0.01 g), and a fragment of each gonad was fixed in Bouin's solution for over 8 h and then transferred to 70% ethanol. Subsequently, the gonads were dehydrated and embedded in paraffin wax. Cross-sections (4–6 μm thick) were obtained in a rotary microtome (Leica RM 2135, Wetzlar, Germany), dyed with haematoxylin and eosin (H&E) and mounted on glass slides for light microscopy inspection. Images were taken using a Nikon Coolpix 4300 digital camera connected to a B941 microscope (Olympus, Tokyo, Japan). Voucher specimens were deposited in the Fish Collection of the Laboratory of Fish Ecology, Universidade Federal Rural do Rio de Janeiro, LEP-UFRRJ#1608-1623. Occurrences of *C. kelberi* in the Lajes Reservoir were made available at the Global

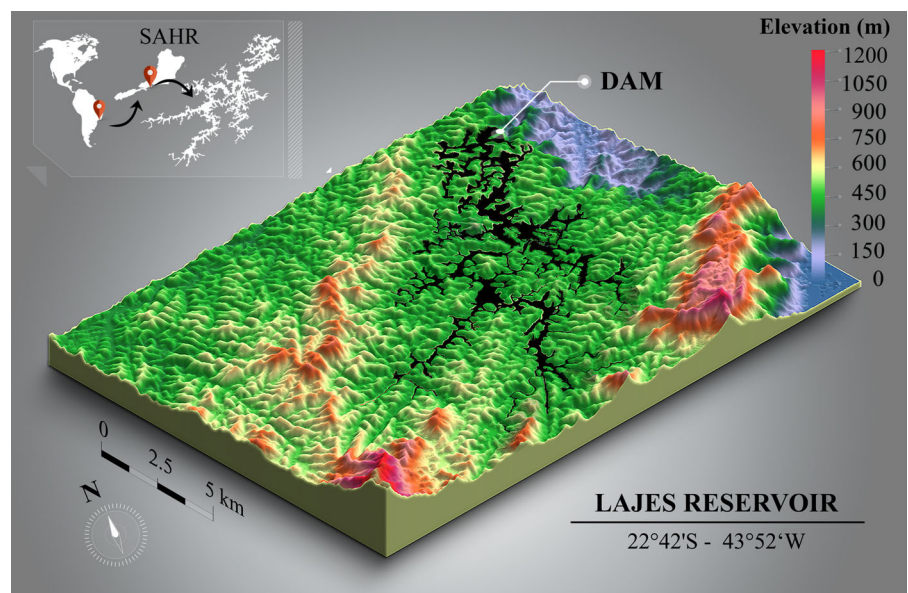


FIGURE 1 Elevation map of the Lajes Reservoir (Rio de Janeiro State, southeastern Brazil) with indication of the drainage basin. SAHR: Southeast Atlantic Hydrographic Region

Biodiversity Facility (Araújo & Guedes, 2020; gbif.org/occurrence/2628729033).

2.3 | Histological characterization

The oocyte stages were defined according to their morphology, affinity to dyes and the occurrence of specific inclusions (e.g., lipid droplets, yolk granules and cortical alveoli). The identification of oocyte stages and postovulatory follicles (POFs) followed Brown-Peterson *et al.* (2011) and adapted to specific histological observations. Accordingly, all vitellogenic and cortical alveolar (CA) oocytes were secondary growth oocytes. Vitellogenesis is a process when important changes occur within the oocyte: size increases noticeably, yolk accumulates in the cytoplasm and several cytoplasmic inclusions appear. In this study, vitellogenic oocytes were classified into three stages, primary (Vtg1), secondary (Vtg2) and tertiary (Vtg3), based on the oocyte size, the volume of cytoplasm filled with yolk globules and the appearance of the zona radiata.

Macroscopic analyses of the gonads were assigned to developmental stages, based on form, size, mass, colour and vascularization. In addition, histological identification of the maturity phases was determined according to the presence/absence of different types of oocytes (i.e., whether organized by ovarian lamellae or not) and spermatocytes. Histological analyses are strongly recommended because the changes observed macroscopically do not exactly reflect the biological events (Honji *et al.*, 2009). The classification of ovaries was based on oocyte stage, thickness of the ovarian wall and the occurrence of different stages of POFs. The diameter of the vitellogenic oocytes and the spermatogenic cell nucleus was determined using the computerized image analyser Image-J 1.48, using 20 non-overlapping random fields of the histological slide prepared for each specimen collected.

2.4 | Data analysis

Differences in the numbers of males and females were tested with a χ^2 test using Yates's correction (Hitchcock, 2009). A logistic curve was adjusted to the data set for assessment of the size at first maturation (L_{50}) and for size when 99% of the individuals reached maturity (L_{99}). Confidence intervals (95%) for L_{50} and L_{99} were estimated using bootstrapping data sets. The differences in logistic regressions of maturity between males and females were tested using a generalized linear model (GLM) adjusted to the binomial error distribution. The significance of terms in a GLM was computed using a χ^2 distribution and summarized in "Analysis of Deviance Table" (for more details: <http://derekogle.com/IFAR/supplements/maturity>; Ogle, 2016).

The following analyses were achieved considering only the individuals that reached L_{50} , i.e., adult individuals (spawning capable, regressing and regenerating), because they transfer part of the obtained energy to the reproductive development. The annual development cycle of the gonads was estimated by changes in the gonado-

somatic index, $I_G = 100(M_G \times M_T^{-1})$, where M_G is the gonad mass and M_T is the total mass. Comparisons of the I_G between the bi-monthly periods were performed using a Kruskal-Wallis non-parametric test. Spearman's correlation coefficient was used to measure the association between I_G (grouped sexes) and the environmental variables (rainfall, water level, transparency and temperature).

3 | RESULTS

A total of 183 specimens (87 females and 96 males) were examined for histological analyses and reproductive indicator calculation (Supporting Information Table S1). The total length (L_T) ranged from 5.8 to 40.0 cm (female) and from 6.0 to 41.1 cm (male). The total mass (M_T) ranged from 0.05 to 1.04 kg (female) and from 0.07 to 1.15 kg (male).

3.1 | Stages of oocyte development

3.1.1 | Primary growth

Oogonia, chromatin nucleolar and perinucleolar stages were present in the ovary throughout the entire annual cycle. Oocyte diameter averaged 90 ± 35 s.d. μm and nucleus 40.6 ± 3.8 μm (Figure 2a,b).

3.1.2 | Secondary growth

CA and vitellogenic oocytes were present in the ovary in the advanced stages of development. Cortical alveoli formation with small vesicles and alveoli appeared in the periphery of the cytoplasm (pre-vitellogenic). The mean diameter of the oocyte and the nucleus was 325 ± 7.8 and 144 ± 6.4 μm , respectively (Figure 2b).

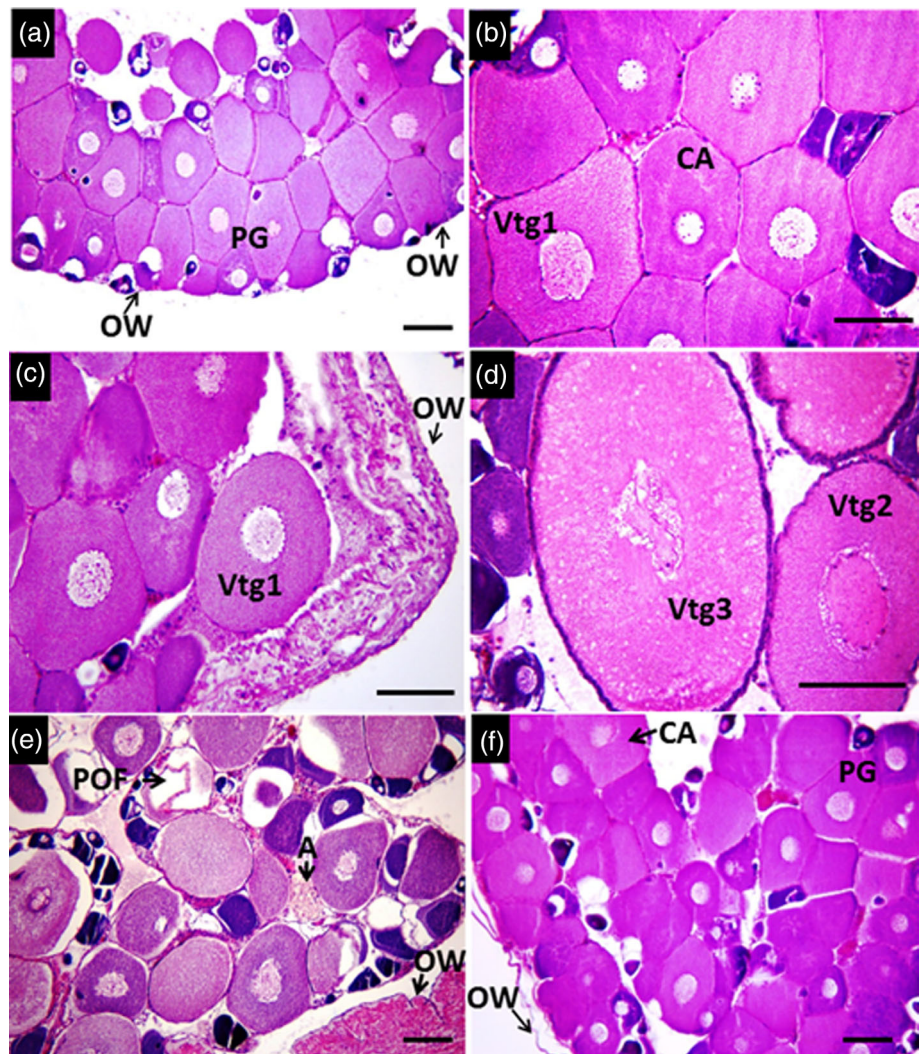
3.1.3 | Vitellogenic

The vitellogenic oocytes were classified into three stages (primary - Vtg1, secondary - Vtg2 and tertiary - Vtg3, Figure 2c,d): primary vitellogenic (Vtg1) - mean oocyte diameter 440 ± 0.8 μm and nucleus 10.7 ± 4.5 μm (Figure 2c-e); secondary vitellogenic (Vtg2) - mean oocyte diameter 588.0 ± 6.6 μm and nucleus 135.0 ± 1.4 μm (Figure 2c); and tertiary vitellogenic (Vtg3) - mean oocyte diameter 770 ± 8.1 μm and nucleus 138.0 ± 1.3 μm (Figure 2d).

3.1.4 | Atresia

During this stage, the cells of the granular layer are in the interior of the cytoplasm, absorbing the yolk. At the end of this stage, the zona radiata disappears. The mean oocyte diameter is 100.0 ± 5.4 μm (Figure 2e,f).

FIGURE 2 Images of ovaries of *Cichla kelberi* in different phases of gonadal maturation. (a) Atresia Immature: oocytes in primary growth (PG), slender ovarian wall (OW), 40x. (b, c) Developing: presence of oocytes of different sizes [cortical alveolar (CA), Vtg1], OW thick, 200x. (d) Spawning capable: predominance of vitellogenic oocytes (Vtg2, Vtg3), 200x. (e) Regressing: presence of different types of oocytes [A, postovulatory follicle (POF)], OW thicker, 100x. (f) Regenerating: oocytes in PG, CA and POF with ovarian thin wall, 100x. Staining: haematoxylin and eosin (HE). Scale bar: 100 μ m



3.2 | Stages of spermatocyte development

The different stages of spermatogenic cells were observed in the interior of the seminiferous tubules during spermatogenesis (spermatogonia, spermatocytes, spermatids and spermatozoa), forming cysts (Figure 3). Each cyst is bound by a layer of connective tissue and contains cells at the same stage of development. The seminiferous tubules are filled with spermatozoa in mature testes.

3.3 | Phases of gonadal maturation

Five phases of gonadal development were identified for the ovaries and testes (Tables 1 and 2). Macroscopic variations were related to gonadal morphology and microscopic histology of the composition of the oocytes and spermatogenic cells (Figures 2 and 3).

The immature phase of ovarian development was characterized by small, narrow, translucent ovaries, occupying around 10% of the celomatic cavity (Table 1). Only oogonia and primary growth (PG) oocytes were present in this phase. The developing phase was

characterized by sack-shaped, opaque ovaries, occupying 15%–20% of the celomatic cavity. Oocytes were present in the different phases of development, mainly CA and Vtg1. Large and voluminous ovaries, yellow to green in colour, characterized the spawning-capable phase, occupying 50% of the celomatic cavity. This phase predominantly had Vtg1 and Vtg2 oocytes. In the regressing phase, the ovaries were flaccid, occupying 40% of the celomatic cavity and showing the presence of follicular atresia and POFs. The regenerating phase was characterized by the presence of small, opaque ovaries, occupying 10% of the celomatic cavity. Most oocytes were in the PG and CA stages.

The immature phase in males (Table 2) was characterized by Sg1 in the germinal epithelium (GE) and by the early formation of testes lobules containing only Sg. The developing phase was characterized by the presence of a continuous GE with spermatocysts undergoing active spermatogenesis and the formation of a lumen in the lobule that is devoid of Sz (Figure 3a,b). The spawning-capable phase consisted of Sz in the lumen of the lobules and in the sperm ducts (Figure 3c,d). The actively spawning subphase for males could be identified only macroscopically and was characterized by the release of milt when gentle pressure was placed on the abdomen (referred to as

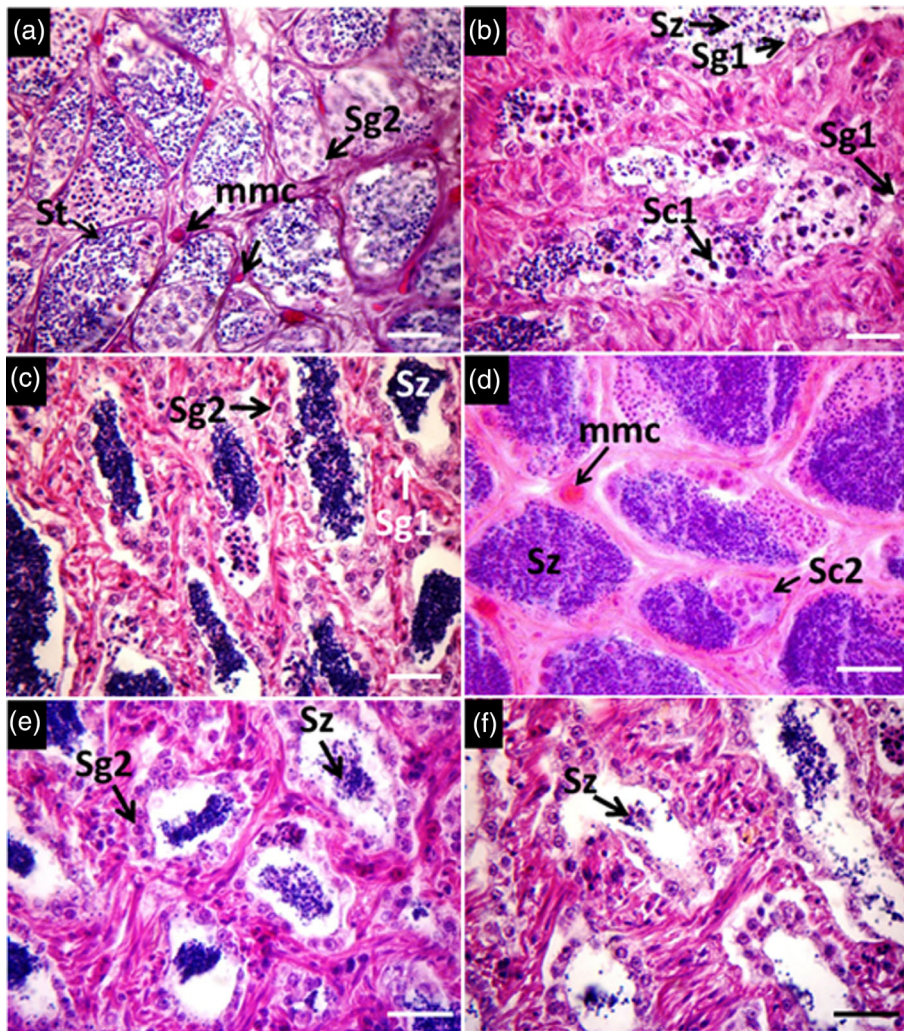


FIGURE 3 Images of testes of *Cichla kelberi* in different phases of gonadal maturation. (a) Regenerating: presence of secondary spermatogonia (Sg2) and melanomacrophage centres (mmc), 100x. (b, c) Developing: various types of spermatocytes evident along lobules (Sg2, Sc1, Sc2, St, Sz) and germinal epithelium (GE) continuous throughout (b - 400x, c, 200x). (d) Spawning capable: predominance of Sz in lumen seminiferous tubules, 200x. (e) Regressing: presence of cysts (Cy), residual spermatozoa (Sz) and GE in regeneration, 200x. (f) Regenerating: proliferation of spermatogonia (Sg1, Sg2) and GE continuous throughout, 200x. Staining: haematoxylin and eosin (HE). Scale bar = 25 µm

“running ripe”). The regressing phase was identified by depleted stores of Sz in the sperm ducts and in the lumen of lobules and by few lobules with spermatocysts (Figure 3e,f), whereas in the regenerating phase, there was a proliferation of spermatogonia (Table 2). Undifferentiated spermatogonia were present along the entire gonad, as well as in the testicular periphery (Figure 3d), where they were isolated among cysts or formed the peripheral clusters, which reappeared in the end of this reproductive phase. At the end of this phase, melanomacrophage centres were observed (Figure 3d).

3.4 | Reproductive characteristics

The sex ratio was well balanced, not differing significantly, 1:1 ($P > 0.05$). The size at first maturation (L_{50}) was 28.6 cm L_T for females (c.i. - c. $L_{95\%} = 27.1$ –30.6 cm L_T) and 30 cm L_T for males (c.i. $L_{95\%} = 28.5$ –32.3 cm L_T , Figure 4). The size at which 99% (L_{99}) of the individuals were mature was 35.7 cm L_T for females (c.i. $L_{95\%} = 30.8$ –40.5 cm L_T) and 40.8 cm L_T for males (c.i. $L_{95\%} = 33.5$ –48.1 cm L_T). No significant differences were found in the maturation logistic curves between the sexes ($\chi^2 = 0.5$, $P = 0.47$).

Females and males in the spawning-capable phase were recorded in all bi-monthly periods, indicating a long reproductive period

(Figure 5). This phase was more frequent in August/September (36.8% in females and 41.6% in males) and in April/May (41.6% in females and 33.3% in males) (Figure 5). The I_G for females and males presented two peaks with different magnitudes (Figure 6). The first and highest peak occurred in August–September (I_G : ♂, 2.62 ± 0.48 ; ♀, 1.32 ± 0.1), the period of low rainfall and temperature and decreasing water level, whereas a second peak occurred in April–May (I_G : ♂, 1.36 ± 0.8 ; ♀, 1.48 ± 0.07), the period of low rainfall and high water level and transparency (Figure 6; Supporting Information Figure S1). Such differences in the I_G among the bi-monthly periods were not significant for both sexes (♂, $\chi^2_{0.05} = 6.48$, $P = 0.16$; ♀, $\chi^2_{0.05} = 5.13$, $P = 0.24$). Nevertheless, significant negative correlations were found between I_G and temperature and between I_G and rainfall, whereas a significant positive correlation was found between I_G and transparency (Figure 7).

4 | DISCUSSION

This study found compelling evidence for an equilibrium reproductive strategy in the non-native predator *C. kelberi* in this isolated reservoir, a likely adaptation over these more than 60 years after its

TABLE 1 Macroscopic and histological description of the phases of the reproductive cycle of female *Cichla kelberi* in the Lajes Reservoir, RJ

Phase	Features of the ovaries	
	Macroscopic	Histological
Immature	Small ovaries, tube shaped, narrow, translucent, occupying around 10% of the celomatic cavity, with weight between 0.1 and 0.2 g, blood vessels indistinct with oocytes little visible to the naked eye.	Only oogonia and PG oocytes present; thin ovarian wall (OW) and little space between oocytes.
Developing	Ovaries present a sack-shaped form, opaque, with colour varying from yellow to orange occupying between 15% and 20% of the celomatic cavity, with weight between 0.5 and 16 g, blood irrigation is regular; many small- and average-sized oocytes were observed, which were opaque and yellow.	Oocytes with different phases of development, mainly pre-vitellogenic (CA), early vitellogenic oocytes (Vtg1) and a few oocytes of the reserve stock; thick OW.
Spawning capable	Large ovaries, voluminous, presents a sack-shaped form, opaque with colouring ranging from yellow to greenish occupying around 50% of the celomatic cavity with weight between 4.9 and 23.2 g, intense vascularization, numerous large opaque and ellipsoid oocytes.	Predominance of oocytes in advanced yolk deposition (Vtg2 and Vtg3), as well as a few oocytes of the reserve stock.
Regressing	Flaccid ovaries, yellow, opaque, sack-shaped occupying 40% of the celomatic cavity with weight between 1.3 and 3.5 g, haemorrhagic, yellow opaque and elliptic oocytes were observed.	Cellular disorganization with the presence of follicular atresia and postovulatory follicles (POFs).
Regenerating	Small ovaries, reddish in colour, opaque occupying around 10% of the celomatic cavity with weight between 1.0 and 1.5 g, with a tubular form and haemorrhagic appearance; blood vessels reduced but present.	PG and CA oocytes present, thick OW, degenerating POFs may be present.

Note: Stages: A: atresia; CA: cortical alveolar; PG: primary growth; POF: postovulatory follicle; Vtg1: primary vitellogenic; Vtg2: secondary vitellogenic; Vtg3: tertiary vitellogenic.

TABLE 2 Macroscopic and histological description of the phases of the reproductive cycle of male *Cichla kelberi* in the Lajes Reservoir, RJ

Phase	Features of the testes	
	Macroscopic	Histological
Immature	Testes were narrow, string like in shape, long, translucent, whitish occupying around 5% of the celomatic cavity with weight between 0.001 and 0.01 g, apparently poorly irrigated.	Small seminiferous tubules present with primary and secondary spermatogonia (Sg1, Sg2).
Developing	Testes were larger and longer than in the previous phase, ribbon shaped, narrow, beige colour, occupying around 15% of the celomatic cavity, with weight between 0.02 and 0.9 g poorly irrigated and extending until the end of the swim bladder.	Seminiferous tubules contain spermatogenic cells at different phases of development (Sc1, Sc2, St).
Spawning capable	Testes were more turgid, with a more elliptical ribbon shape, present a whitish colouring, opaque occupying around 30% of the celomatic cavity, wide and long with weight between 1.5 and 3.8 g, highly irrigated; it was possible to observe semen when the testicle was pressed.	Most spermatozoa (Sz) in the lumen of lobules and/or sperm ducts, little amount of Sc2; presence of melano-macrophage centres (mmc).
Regressing	Flaccid, filiform and long testes, narrow thickness, demonstrate a reddish colouring with weight between 0.09 and 2 g, haemorrhagic.	Spermatozoa (Sz) present in the lumen of disorganized, empty seminiferous tubules but still have some seminiferous tubules with a small quantity of spermatozoa (Sz).
Regeneration	Small and filiform testes, pale cream, more consistent than the previous phase with weight between 0.01 and 0.1 g.	

Note: Stages: Sg1: primary spermatogonia; Sg2: secondary spermatogonia; Sc1: primary spermatocyte; Sc2: secondary spermatocyte; St: spermatid; Sz: spermatozoa.

introduction. Spawning occurred in parcels and extended over a long period during the year. Other features of the ovaries and vitellogenic oocytes coincided with the equilibrium reproductive strategy of *C. kelberi*, such as multiple spawning, adhesive eggs and parental care.

The testicular type is lobular, and the distribution of undifferentiated spermatogonia cells characterizes the testes as the type unrestricted spermatogonial according to Grier *et al.* (1980). This pattern is in accordance with those reported by de Siqueira-Silva *et al.* (2013) that

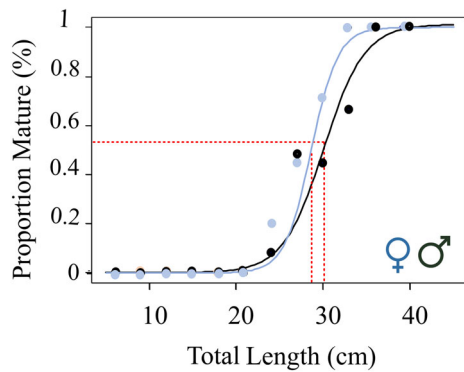


FIGURE 4 Logistic regression adjusted for the proportion of mature *Cichla kelberi* by total length (L_+) at 3 cm intervals. Males and females are indicated in black and light blue, respectively. Estimation of L_{50} is shown in the dotted red lines

described the testes in *C. kelberi* as unrestricted spermatogonial lobular, an apomorphic characteristic in the recent groups of teleosts. More recently, de Siqueira-Silva *et al.* (2019) reported that among the unrestricted type, an intermediate variation in spermatogonial distribution was observed in *C. kelberi* because although distributed along the entire length of the GE, undifferentiated spermatogonia accumulate at the blind end of the lobules, close to the tunica albuginea. Unrestricted lobular testis was also reported in other cichlids such as *Cichlasoma dimerus* (Heckel, 1840) by Vázquez *et al.* (2012) and *Cichla intermedia* Machado-Allison, 1971, by de Siqueira-Silva (de Siqueira-Silva *et al.*, 2019). This structure seems to be common to other species of the family Cichlidae, such as *Labeotropheus trewasae* Fryer, 1956, *Pterophyllum scalare* (Schultze, 1823) and *Oreochromis aureus* (Steindachner, 1864) (Grier *et al.*, 1980; Parenti & Grier, 2004). The gonadal restructuration and the spermatogonial proliferation of *C. kelberi* gather at the same time, thus explaining the absence of individuals totally spent after their first reproductive cycle de Siqueira-Silva *et al.* (2013). In addition, females and males in the spawning-capable phase were observed throughout the year, and spawned females with ovaries with empty and atresic follicles together with oocytes in the four stages of development were observed, indicating that the species spawns in parcels (batch spawn).

Batch spawning over a long period contributes to the reduction in competition among larvae and, after that, among juveniles. Other advantages of batch spawning include increased fertility, dilution of the risk of loss of offspring due to predation or unfavourable environmental conditions (McEvoy & McEvoy, 1992). This type of spawning has been reported for species of *Cichla* in another reservoir in south-eastern (Souza *et al.*, 2008) and northeast Brazil (Chellappa *et al.*, 2003). Nevertheless, in natural habitats such as the Amazonian rivers, environmental and resource fluctuations can induce marked reproductive seasonality (Jepsen *et al.*, 1999; Lowe-McConnell, 1969) and total spawning (Souza *et al.*, 2011). The variation in spawning types between environments (natural vs. reservoirs) may be associated with the energy cost to defend the youngs, which is possibly higher in natural habitats because of the presence of natural predators and competitors (Jepsen *et al.*, 1999).

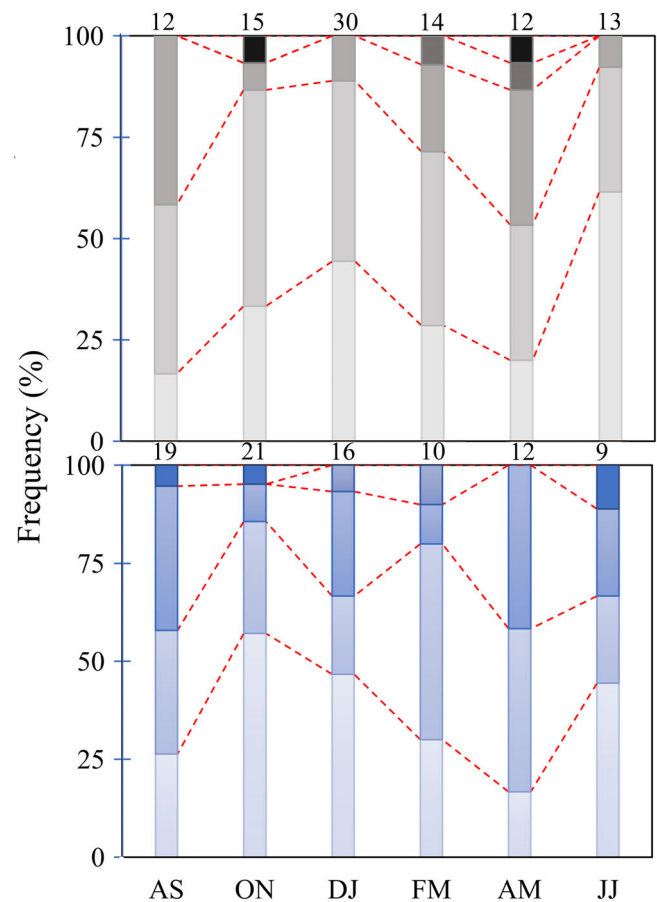


FIGURE 5 Bi-monthly changes in frequency distribution of the reproductive phases of female (above) and male (below) *Cichla kelberi*. The number of individuals is indicated above each bar. A/S: August/September; O/N: October/November; D/J: December/January; F/M: February/March; A/M: April/May; J/J: June/July. (♂♀); (■) Regression, (■) Regenerating, (■) Spawning Capable, (■) Developing, (■) Immature

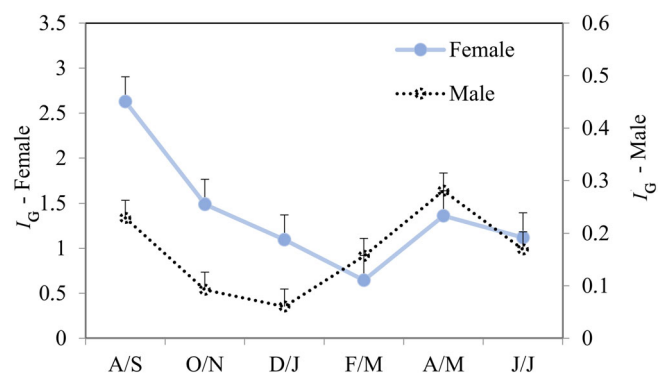


FIGURE 6 Bi-monthly changes in the gonado-somatic index (means + s.d.) for female and male *Cichla kelberi* in the Lajes Reservoir caught between August 2015 and July 2016. Males and females separated are indicated in black and light blue, respectively. (—) Female, (---) Male

A balanced sex ratio was found for *C. kelberi* in the Lajes Reservoir. The sex ratio varies considerably among the non-native populations of *Cichla* spp. (e.g., Chellappa *et al.*, 2003; Jepsen

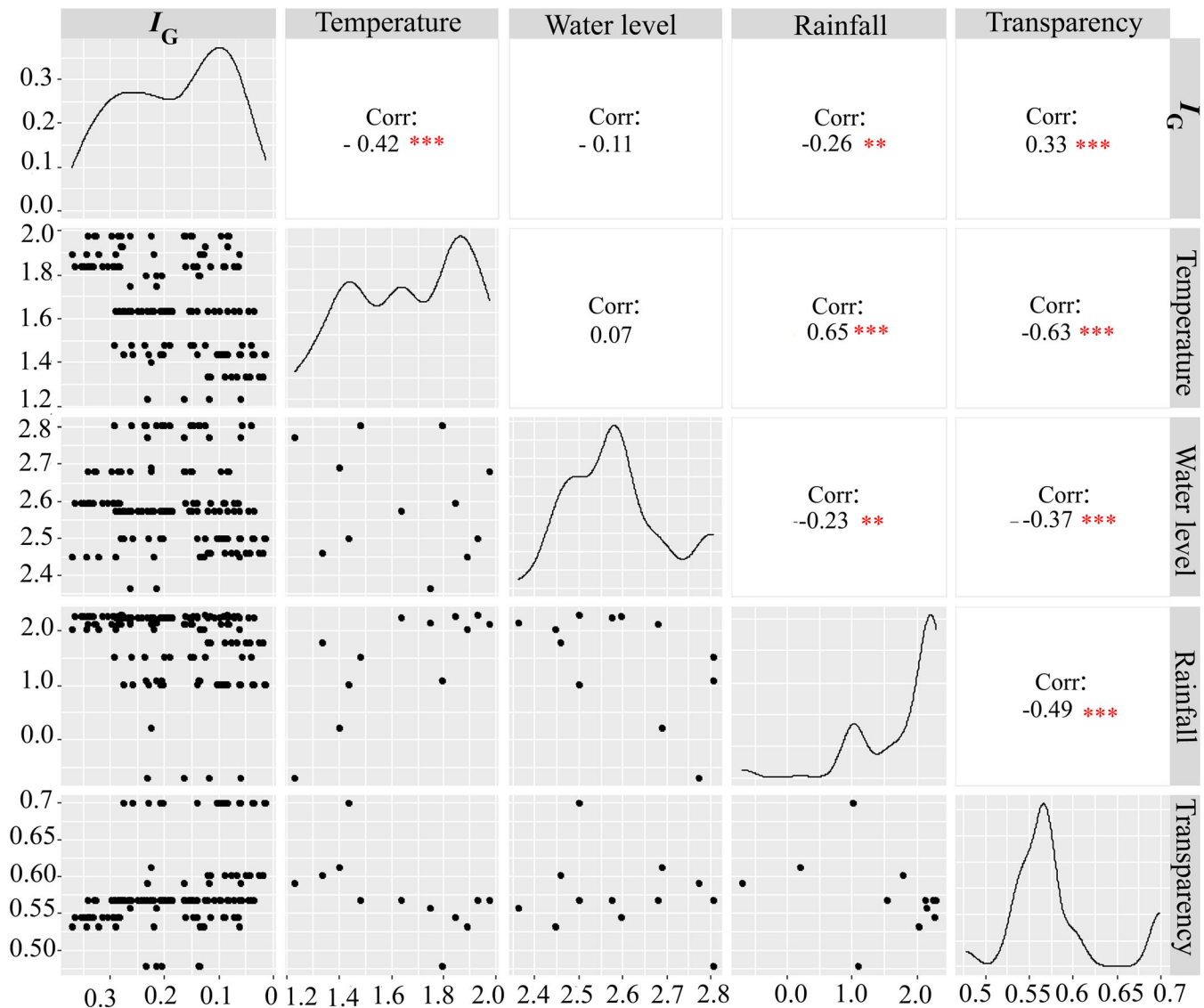


FIGURE 7 Scatterplot diagram and trend line for Spearman's correlation coefficients between the gonado-somatic index I_G (vertical axis) and environmental variables (horizontal axis); logarithm₁₀ transformed data

et al., 1999; Souza et al., 2008; Vieira et al., 2009; Zaret, 1980). Jepsen et al. (1999) reported, e.g., that males were almost twice as numerous as females, whereas Souza et al. (2008) reported that females were almost thrice as numerous as males. Nevertheless, there is no apparent explanation for this divergent pattern. Generally, sex ratio can be affected over time and space by differentiated mortality for males and females, competition for partners, environmental pollutants, among other factors (Jennions & Fromhage, 2017). Regarding size at first maturation, the values found for *C. kelberi* in the present study ($\varphi = 27.1\text{--}30.6$ and $\delta = 28.5\text{--}32.3$ cm L_T) were relatively higher than those observed for *Cichla* spp. in other reservoirs in southeastern Brazil ($\delta = 19.2\text{--}21.5$ and $\varphi = 20.7\text{--}23.5$ cm L_T , minimum–maximum) as reported by Chellappa et al. (2003), Gomiero and Braga (2004a), Gomiero et al. (2009), Luiz et al. (2011) and Souza et al. (2008). The stable hydrological conditions and low densities of predators and native competitors in the Lajes Reservoir, e.g., could have favoured a

greater investment in somatic growth before reproduction. On the contrary, the population of *C. kelberi* in the Lajes Reservoir is particularly exposed to sport fishing and cannibalism (Santos et al., 2011), factors known to negatively affect the maturation size in fish (Enberg et al., 2012). Therefore, it is crucial to understand how stable hydrological conditions, fishing and cannibalism, interact and affect the first maturation size. It is a complex task which should be better understood in future studies.

C. kelberi had a long reproductive period in the Lajes Reservoir, with mature females and males coexisting with specimens at different stages of gonadal development throughout the year. Local environmental features, such as clear water (transparency >3.5 m), high retention time (300 days), predominance of lentic conditions, low-level fluctuation (≈ 4 m during the study period) and high availability of spawning substrates, are characteristics that make this reservoir a relatively stable environment and conducive to the long breeding period

found for *C. kelberi*. The observation of mature males and females during most of the year seems to be a general consensus for non-native *Cichla* populations in altered environments in Brazil (Chellapa *et al.*, 2003; Gomiero & Braga, 2004a; Gomiero *et al.*, 2009; Vieira *et al.* 2009; Normando *et al.* 2009; Luiz *et al.*, 2011; Souza *et al.*, 2008), the United States (Shafland, 1999) and Panama (Zaret, 1980). A similar pattern was also reported for populations in native ranges of distribution (but impacted by dams), as in the cases of *Cichla piquiti* Kullander & Ferreira, 2006, in the Lajeado Reservoir (Tocantins-Araguaia River basin; Marto *et al.*, 2015) and *Cichla vazzoleri* Kullander & Ferreira, 2006, in the Balbina Reservoir (Central Amazon; Horie, 2013). Although these studies in altered environments indicate that reproduction can potentially occur over a long period, reproductive peaks vary considerably within and between populations, at times and under contrasting environmental conditions. The long reproductive period observed in this study for *C. kelberi* is corroborated with other populations, suggesting a strong invasive potential of non-native populations of *Cichla* and the ability to adapt to different hydroclimate conditions.

In the case of natural populations in environments preserved in the Amazon biome (with dams absent), there is evidence of a different reproductive pattern, with greater seasonality associated with the period of rain/flood in well-defined annual cycles (Jepsen *et al.*, 1999; Lowe-McConnell, 1969; Muñoz *et al.*, 2006; Santos *et al.*, 2011; Winemiller, 2001). These differences observed between native populations in conserved areas (more defined seasonal cycle) and native or non-native populations in altered areas (less-defined seasonal cycle) may be related to changes in the cyclical flood pattern of habitats imposed by dams (Hurd *et al.*, 2016; Junk, 1989), decreasing environmental seasonality, favouring an equilibrium strategy (Mims & Olden, 2012). The construction of reservoirs facilitates the establishment of aquatic non-native species, which are 2.4–300 times more likely to occur in impoundments than in natural lakes (Johnson *et al.*, 2008). Reproductive plasticity within a balance strategy can make populations resilient or even anti-fragile, *i.e.*, not only support environmental changes imposed by dams but also benefit from them.

The reproductive success and the establishment of non-native populations of *Cichla* spp. have caused severe and widespread impacts on native communities. Demographic dynamics of *C. kelberi*, especially juvenile pulse periods, is one of the main factors underlying the loss of diversity (Pelicice *et al.*, 2015). Even the presence of refuges, such as aquatic macrophytes, does not seem to be sufficient to limit the impact on native prey (Kovalenko *et al.*, 2010). In addition, prey seems to exhibit low morphological response (Geladi *et al.*, 2019) to a predator with variable vision in variable environments (Escobar-Camacho *et al.*, 2019). Prey collapse, reduction in abundance, loss of small fish and other damage persisted for several decades because of the introduction of *Cichla* species in tropical areas (Sharpe *et al.*, 2017). The preference for small prey and juveniles is related to limitations imposed by the morphology of the digestive tract of adults (Burress & Wainwright, 2020), which means that many sympatric fish are not proportionally consumed (Hill *et al.*, 2004). A key issue is to understand how *Cichla* maintains self-sustaining populations in the long

term even after resource depletion. Cannibalism seems to be one of the main keys to answering this question, and a long reproductive period can be the basis for this strategy. In the Lajes Reservoir, *e.g.*, cannibalism rates (adults preying on juveniles) are high and reach up to 54.2% of the index of relative importance (Santos *et al.*, 2011). Cannibalism is more intense in non-native populations, especially in reservoirs, where resources are less abundant or have been primarily uprooted by excessive predation (Pereira *et al.*, 2017). The highest rates of cannibalism occur during the reproduction peak (*e.g.*, Santos, 2001; Gomiero & Braga, 2004b). It is particularly interesting that behaviour that seems so contrary to care—*i.e.*, eating one's young—can in some cases broaden the conditions under which care can evolve (Klug & Bonsall, 2019). In this context, a long reproductive period can make cannibalism viable throughout the year. This complex retro-feeding (*i.e.*, reproducing and eating) can circumvent resource scarcity in reservoirs, make populations self-sustaining in the long run and further complicate management.

Overall, peacock bass has reproductive characteristics associated with sedentary local populations, long breeding seasons and parental care which fit to the equilibrium strategy (Winemiller, 1989). Evidence suggests that equilibrium strategy is associated with decreased hydrological variability and increasing environmental stability (Mims & Olden, 2012). Reservoir construction interrupts river continuity, creates new lentic environments and commonly promotes greater water stability. Franco *et al.* (2018) reported that increased reservoir water retention time, when combined with warmer and more transparent waters, can increase the abundance of peacock bass. The advantage of the strategy of equilibrium in altered environments may be associated to the fact that the lentic conditions and greater hydrological stability of the reservoirs promote adequate conditions for nest building and protection of juveniles (Marto *et al.*, 2015; Muñoz *et al.*, 2006; Winemiller, 2001). Consequently, the strategy of equilibrium and plasticity in reproductive traits may be the main factors inherent in the successful colonization and settlement of the peacock bass in the environments in which the species were introduced.

ACKNOWLEDGEMENTS

This work was supported by FAPERJ – Fundação Carlos Chagas de Amparo à Pesquisa do Estado do Rio de Janeiro through the grant Cientista do Nosso Estado to F.G.A. (Proc. E-26/201.248/2014). Light Energia S.A. provided infrastructure and financial support (contract number 4600004989) through a monitoring programme of the ichthyofauna of the Lajes Reservoir.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

I.D.G. and G.H.S.G. conceived the study; G.H.S.G., A.A.N. and F.S.A. participated in the fieldwork; F.G.A., A.A.N. and G.H.S.G. analysed the data; F.G.A. and G.H.S.G. wrote the manuscript, with contributions from I.D.G. and F.S.A.

COMPLIANCE WITH ETHICAL STANDARDS

The authors state that the research was conducted according to ethical standards.

AVAILABILITY OF DATA

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Gustavo Henrique Soares Guedes  <https://orcid.org/0000-0001-8155-8337>

Iracema David Gomes  <https://orcid.org/0000-0002-7985-6068>

Aparecida Alves do Nascimento  <https://orcid.org/0000-0002-0970-7649>

Fernanda Silva de Aguiar  <https://orcid.org/0000-0002-6050-2366>

Francisco Gerson Araújo  <https://orcid.org/0000-0003-4551-1974>

REFERENCES

- Agostinho, A. A., Gomes, L. C., Verissimo, S., & Okada, E. K. (2004). Flood regime, dam regulation and fish in the Upper Paraná river: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, 14, 11–19. <https://doi.org/10.1007/s11160-004-3551-y>.
- Araújo, F. G., & Santos, L. N. (2001). Distribution of fish assemblages in the Lajes Reservoir, Rio de Janeiro, Brazil. *Brazilian Journal of Biology*, 61, 563–576. <https://doi.org/10.1590/S1519-69842001000400006>.
- Araújo, F. G., Guedes, G. H. S. (2020). Base de dados da Coleção Ictiológica do LEP-UFRRJ. Version 1.3. Sistema de Informação sobre a Biodiversidade Brasileira - SiBBR. <https://doi.org/10.15468/srsucy>. Retrieved from <https://www.gbif.org/occurrence/2628729033>.
- Brown-Peterson, N. J., Wyanski, D. M., Saborido-Rey, F., Macewicz, B. J., & Lowerre-Barbieri, S. K. (2011). A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 3, 52–70. <https://doi.org/10.1080/19425120.2011.555724>.
- Burress, E. D., & Wainwright, P. C. (2020). A peacock bass (*Cichla*) functional novelty relaxes a constraint imposed by the classic cichlid pharyngeal jaw innovation. *Biological Journal of the Linnean Society*, 130(2), 382–394. <https://doi.org/10.1093/biolinnean/blaa050>.
- Carvalho, D. C., Oliveira, D. A. A., Sampaio, A., & Beheregaray, L. B. (2014). Analysis of propagule pressure and genetic diversity in the invasibility of a freshwater apex predator: the peacock bass (genus *Cichla*). *Neotropical Ichthyology*, 12, 105–116. <https://doi.org/10.1590/S1679-62252014000100011>.
- Chellappa, S., Câmara, M. R., Chellappa, N. T., Beveridge, M. C. M., & Huntingford, F. A. (2003). Reproductive ecology of a neotropical cichlid fish, *Cichla monoculus* (Osteichthyes: Cichlidae). *Brazilian Journal of Biology*, 63, 17–26. <https://doi.org/10.1590/S1519-69842003000100004>.
- Chong, V. C., Lee, P. K. Y., & Lau, C. M. (2010). Diversity, extinction risk and conservation of Malaysian fishes. *Journal of Fish Biology*, 76, 2009–2066. <https://doi.org/10.1111/j.1095-8649.2010.02685.x>.
- Darwin, C. R. (1889). *The descent of man, and selection in relation to sex* (pp. 338–341). New York, NY: D. Appleton and Company. http://darwin-online.org.uk/converted/pdf/1889_Descent_F969.pdf.
- de Siqueira-Silva, D. H., Rodrigues, M. S., & Nóbrega, R. H. (2019). Testis structure, spermatogonial niche and Sertoli cell efficiency in Neotropical fish. *General and Comparative Endocrinology*, 273, 218–226. <https://doi.org/10.1016/j.ygcen.2018.09.004>.
- de Siqueira-Silva, D. H., Vicentini, C. A., Ninhaus-Silveira, A., & Verissimo-Silveira, R. (2013). Reproductive cycle of the neotropical cichlid yellow peacock bass *Cichla kelberi*: A novel pattern of testicular development. *Neotropical Ichthyology*, 11, 587–596. <https://doi.org/10.1590/S1679-62252013000300012>.
- Dicionário Ilustrado Tupi-Guarani. (2019). Retrieved from <http://www.dicionariotupiguarani.com.br/>.
- Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, Ø., Boukal, D. S., Baulier, L., ... Heino, M. (2012). Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. *Marine Ecology*, 33, 1–25. <https://doi.org/10.1111/j.1439-0485.2011.00460.x>.
- Escobar-Camacho, D., Pierotti, M. E. R., Ferenc, V., Sharpe, D. M. T., Ramos, E., Martins, C., & Carleton, K. L. (2019). Variable vision in variable environments: The visual system of an invasive cichlid (*Cichla monoculus*) in Lake Gatun, Panama. *The Journal of Experimental Biology*, 222, jeb188300. <https://doi.org/10.1242/jeb.188300>.
- Franco, A. C. S., Santos, L. N., Petry, A. C., & García-Berthou, E. (2018). Abundance of invasive peacock bass increases with water residence time of reservoirs in southeastern Brazil. *Hydrobiologia*, 817, 155–166. <https://doi.org/10.1007/s10750-017-3467-x>.
- Geladi, I., De León, L. F., Torchin, M. E., Hendry, A. P., González, R., & Sharpe, D. M. T. (2019). 100-year time series reveal little morphological change following impoundment and predator invasion in two Neotropical characids. *Evolutionary Applications*, 12(7), 1385–1401. <https://doi.org/10.1111/eva.12763>.
- Golani, D., Sonin, O., Snovsky, G., David, L., & Tadmor-Levi, R. (2019). The occurrence of the peacock bass (*Cichla kelberi* Kullander and Ferreira 2006) in Lake Kinneret (Sea of Galilee), Israel. *BiolInvasions Records*, 8, 706–711. <https://doi.org/10.3391/bir.2019.8.3.28>.
- Gomiero, L. M., & Braga, F. M. S. (2004a). Reproduction of species of the genus *Cichla* in a reservoir in Southeastern Brazil. *Brazilian Journal of Biology*, 64(3), 613–624. <https://dx.doi.org/10.1590/S1519-69842004000400008>.
- Gomiero, L. M., & Braga, F. M. S. (2004b). Cannibalism as the main feeding behaviour of tucunares introduced in Southeast Brazil. *Brazilian Journal of Biology*, 64(3), 625–632. <https://doi.org/10.1590/S1519-69842004000400009>.
- Gomiero, L. M., Villares, G. A., Jr., & Naous, F. (2009). Reproduction of *Cichla kelberi* (Kullander and Ferreira, 2006) introduced into an artificial lake in south-eastern Brazil. *Brazilian Journal of Biology*, 69, 175–183. <https://doi.org/10.1590/S1519-69842009000100023>.
- Grier, H. J., Linton, J. R., Leatherland, J. F., & Vlaming, V. L. (1980). Structural evidence for two difference testicular types in teleost fishes. *American Journal of Anatomy*, 159, 331–345. <https://doi.org/10.1002/aja.1001590307>.
- Guedes, G. H. S., Mattos, T. M., Camilo, G. S., Uehara, W., Ferreira, D. L. P., & Araújo, F. G. (2020). Artificial flow regime promotes abiotic and biotic gradients: Testing the concept of longitudinal zonation in an off-river reservoir. *Ecology & Hydrobiology*, 20(2), 256–264. <https://doi.org/10.1016/j.ecohyd.2020.02.002>.
- Guarino, A. W. S., Branco, C. W. C., Diniz, G. P., & Rocha, R. (2005). Limnological studies in an old tropical reservoir (Lajes Reservoir, RJ, Brazil). *Acta Limnologica Brasiliensia*, 17, 129–141. Retrieved from [http://www.ablimno.org.br/acta/pdf/acta_limnologica_contents1702E_files/Acta17\(2\)_03.pdf](http://www.ablimno.org.br/acta/pdf/acta_limnologica_contents1702E_files/Acta17(2)_03.pdf).
- Hitchcock, D. B. (2009). Yates and Contingency Tables: 75 years later. *Electronic Journal for History of Probability and Statistics*, 5(2), 1–14. Retrieved from <http://www.jehps.net/Decembre2009/Hitchcock.pdf>.
- Hill, J. E., Nico, L. G., Cichra, C. E., & Gilbert, C. R. (2004). Prey vulnerability to peacock cichlids and largemouth bass based on predator gape and prey body depth. *Proceedings of the Annual Conference of the South-Eastern Association of Fish and Wildlife Agencies*, 58, 47–56. Retrieved from <https://pubs.er.usgs.gov/publication/70161786>.
- Honji, R., Narcizo, A., Borella, M., Romagosa, E., & Moreira, R. (2009). Patterns of oocyte development in natural habitat and captive *Salminus hilarii* Valenciennes, 1850 (Teleostei: Characidae). *Fish Physiology and*

- Biochemistry*, 35, 109–123. <https://doi.org/10.1007/s10695-008-9239-9>.
- Horie, C. A. C. (2013). Biologia reprodutiva e estrutura da população do tucunaré *Cichla vazzoleri* (perciformes: cichlidae) no reservatório da hidrelétrica de Balbina, Amazonas, Brasil (Masters Thesis). Retrieved from <https://repositorio.inpa.gov.br/>.
- Hurd, L. E., Sousa, R. G. C., Siqueira-Souza, F. K., Cooper, G. J., Kahn, J. R., & Freitas, C. E. C. (2016). Amazon floodplain fish communities: Habitat connectivity and conservation in a rapidly deteriorating environment. *Biological Conservation*, 195, 118–127. <https://doi.org/10.1016/j.biocon.2016.01.005>.
- Jennions, M. D., & Fromhage, L. (2017). Not all sex ratios are equal: the Fisher condition, parental care and sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372, 20160312. <https://doi.org/10.1098/rstb.2016.0312>.
- Jepsen, D. B., Winemiller, K. O., Taphorn, D. C., & Rodriguez Olarte, D. (1999). Age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela. *Journal of Fish Biology*, 55, 433–450. <https://doi.org/10.1111/j.1095-8649.1999.tb00689.x>.
- Johnson, P. T., Olden, J. D., & Vander Zanden, M. J. (2008). Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment*, 6, 357–363. <https://doi.org/10.1890/070156>.
- Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication in Fisheries and Aquatic Sciences*, 106, 110–127.
- Kovalenko, K. E., Dibble, E. D., Agostinho, A. A., & Pelicice, F. M. (2010). Recognition of non-native peacock bass, *Cichla kelberi* by native prey: testing the naiveté hypothesis. *Biological Invasions*, 12, 3071–3080. <https://doi.org/10.1007/s10530-010-9698-7>.
- Kullander, S. O., & Ferreira, E. J. G. (2006). A review of the South American cichlid genus *Cichla*, with descriptions of nine new species (Teleostei: Cichlidae). *Ichthyological Exploration of Freshwaters*, 17, 289–398. ISBN: 9783899370645.
- Klug, H., & Bonsall, M. B. (2019). Coevolution influences the evolution of filial cannibalism, offspring abandonment and parental care. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191419. <https://doi.org/10.1098/rspb.2019.1419>.
- Lowe-McConnell, R. H. (1969). The cichlid fishes of Guyana, South America, with note on their ecology and breeding behavior. *Zoological Journal of the Linnaean Society*, 48, 255–302. <https://doi.org/10.1111/j.1096-3642.1969.tb00714.x>.
- Luiz, T. F., Velludo, M. R., Peret, A. C., Rodrigues-Filho, J. L., & Peret, A. M. (2011). Diet, reproduction and population structure of the introduced Amazonian fish *Cichla piquiti* (Perciformes: Cichlidae) in the Cachoeira Dourada reservoir (Paranaíba River, central Brazil). *Journal de Biologia Tropical*, 59, 727–741. <https://doi.org/10.15517/rbt.v0i0.3135>.
- Maciulek, J. A. (1984). Exotic fishes in Hawaii and other islands of Oceania. In W. R. Courtenay & J. R. Stauffer (Eds.), *Distribution, biology and management of exotic fishes* (pp. 131–161). Baltimore: John Hopkins University Press. Retrieved from <https://pubs.er.usgs.gov/publication/70162156>.
- McEvoy, L. A., & McEvoy, J. (1992). Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. *Journal of Fish Biology*, 41, 125–136. <https://doi.org/10.1111/j.1095-8649.1992.tb03874.x>.
- Marto, V. C. O., Akama, A., & Pelicice, F. M. (2015). Feeding and reproductive ecology of *Cichla piquiti* Kullander & Ferreira, 2006 within its native range, Lajeado reservoir, rio Tocantins basin. *Neotropical Ichthyology*, 13, 625–636. <https://doi.org/10.1590/1982-0224-20140165>.
- Menezes, R. F., Attayde, J. L., Lacerot, G., Kosten, S., Souza, C., Costa, L. S., ... Jeppsen, E. (2012). Lower biodiversity of native fish but only marginally altered plankton biomass in tropical lakes hosting introduced piscivorous *Cichla cf. ocellaris*. *Biological Invasions*, 14, 1353–1363. <https://doi.org/10.1007/s10530-011-0159-8>.
- Mims, M. C., & Olden, J. D. (2012). Life history theory predicts fish assemblage response to hydrologic regimes. *Ecology*, 93, 35–45. <https://doi.org/10.1890/11-0370.1>.
- Muñoz, H., Van Damme, P. A., & Duponchelle, F. (2006). Breeding behaviour and distribution of the tucunaré *Cichla aff. monoculus* in a clear water river of the Bolivian Amazon. *Journal of Fish Biology*, 69, 1018–1030. <https://doi.org/10.1111/j.1095-8649.2006.01177.x>.
- Normando, F. T., Arantes, F. P., Luz, K. K., Thomé, R. G., Rizzo, E., Sato, Y., & Bazzoli, N. (2009). Reproduction and fecundity of tucunaré, *Cichla kelberi* (Perciformes: Cichlidae), an exotic species in Três Marias Reservoir, southeastern Brazil. *Journal of Applied Ichthyology*, 25, 299–305. <https://doi.org/10.1111/j.1439-0426.2008.01174.x>.
- Ogle, D. (2016). *Introductory Fisheries Analyses with R*. New York: Chapman and Hall/CRC. <https://doi.org/10.1201/9781315371986>.
- Parenti, L. R., & Grier, H. J. (2004). Evolution and phylogeny of gonad morphology in bony fishes. *Integrate Comparative Biology*, 44, 333–348. doi: 10.1093/icb/44.5.333.
- Pelicice, F. M., & Agostinho, A. A. (2009). Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. *Biological Invasions*, 11, 1789–1801. <https://doi.org/10.1007/s10530-008-9358-3>.
- Pelicice, F. M., Latini, J. D., & Agostinho, A. A. (2015). Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. *Hydrobiologia*, 746, 271–283. <https://doi.org/10.1007/s10750-014-1911-8>.
- Pereira, L. S., Agostinho, A. A., & Winemiller, K. O. (2017). Revisiting cannibalism in fishes. *Reviews in Fish Biology and Fisheries*, 27, 499–513. <https://doi.org/10.1007/s11160-017-9469-y>.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., ... Stromberg, J. C. (1997). The natural flow regime. *BioScience*, 47, 769–784. <https://doi.org/10.2307/1313099>.
- Reis, R. E., Albert, J. S., Di Dario, F., Mincarone, M. M., Petry, P., & Rocha, L. A. (2016). Fish biodiversity and conservation in South America. *Journal of Fish Biology*, 89, 12–47. <https://doi.org/10.1111/jfb.13016>.
- Santos, L. N., Gonzalez, A. F., & Araújo, F. G. (2001). Dieta do tucunaré-amarelo *Cichla monoculus* (Bloch & Schneider) (Osteichthyes, Cichlidae), no Reservatório de Lajes, Rio de Janeiro, Brasil. *Revista Brasileira de Zoologia*, 18(1), 191–204. <https://doi.org/10.1590/S0101-81752001000500015>.
- Santos, A. F. G. N., Santos, L. N., & Araújo, F. G. (2011). Feeding morphology of the neotropical piscivorous fish *Cichla kelberi* (Perciformes: Cichlidae) introduced into an oligotrophic Brazilian reservoir. *Revista de Biologia Tropical*, 59, 1245–1255.
- Santos, A. F. G. N., Santos, L. N., & Araújo, F. G. (2004). Water level influences on body condition of *Geophagus brasiliensis* (Perciformes, Cichlidae) in a Brazilian oligotrophic reservoir. *Neotropical Ichthyology*, 2, 151–156. <https://doi.org/10.1590/S1679-62252004000300007>.
- Shafland, P. L. (1999). The introduced butterfly peacock (*Cichla ocellaris*) in Florida. II. Food and reproductive biology. *Reviews in Fisheries Science*, 7, 95–113. <https://doi.org/10.1080/10641269991319207>.
- Sharpe, D. M. T., De León, L. F., González, R., & Torchin, M. E. (2017). Tropical fish community does not recover 45 years after predator introduction. *Ecology*, 98, 412–424. <https://doi.org/10.1002/ecy.1648>.
- Soares, M., Marinho, M., Huszar, V., Branco, C., & Azevedo, S. (2008). The effects of water retention time and watershed features on the limnology of two tropical reservoirs in Brazil. *Lakes & Reservoirs: Research & Management*, 13, 257–269. <https://doi.org/10.1111/j.1440-1770.2008.00379.x>.
- Souza, J. E., Fragoso-Moura, E. M., Fenerich-Verani, N., Rocha, O., & Verani, J. R. (2008). Population structure and reproductive biology of *Cichla kelberi* (Perciformes, Cichlidae) in Lobo Reservoir, Brazil. *Neotropical Ichthyology*, 6, 201–210. <https://doi.org/10.1590/S1679-62252008000200007>.

- Souza, R. L., Silva, D. L., Valladares, A. C. P., Rocha, R. M., Ferreira, M. A. P., & Queiroz, H. L. (2011). Gonadal development of the peacock bass *Cichla monoculus* (Perciformes: Cichlidae) in the middle Solimões. *Uakari*, 7(1), 41–55. <https://doi.org/10.31420/uakari.v7i1.98>.
- Vázquez, G. R., Da Cuña, R. H., Meijide, F. J., & Guerrero, G. A. (2012). Spermatogenesis and changes in testicular structure during the reproductive cycle in *Cichlasoma dimerus* (Teleostei, Perciformes). *Acta Zoologica*, 93, 338–350. <https://doi.org/10.1111/j.1463-6395.2011.00508.x>.
- Vieira, A. B. C., Salvador, L. F., Jr., Melo, R. M. C., Santos, G. B., & Bazzoli, N. (2009). Reproductive biology of the peacock bass *Cichla piquiti* (Perciformes: Cichlidae), an exotic species in a Neotropical reservoir. *Neotropical Ichthyology*, 7, 745–750. <https://doi.org/10.1590/S1679-62252009000400024>.
- Welcomme, R. L. (1988). International introductions of inland aquatic species. Food and Agriculture Organization of the United Nations, *FAO Fisheries Technical Paper*, 294, Rome. Retrieved from <http://www.fao.org/3/X5628E/X5628E00.htm>
- Willis, S. C., Nunes, M. S., Montaña, C. G., Farias, P. F., & Lovejoy, N. R. (2007). Systematics, biogeography and evolution of the Neotropical peacock basses *Cichla* (Perciformes, Cichlidae). *Molecular Phylogenetics and Evolution*, 44, 291–307. <https://doi.org/10.1016/j.ympev.2006.12.014>.
- Winemiller, K. O. (1989). Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia*, 81, 225–241. <https://doi.org/10.1007/BF00379810>.
- Winemiller, K. O. (2001). Ecology of peacock cichlids (*Cichla* spp.) in Venezuela. *Journal of Aquaculture and Aquatic Sciences*, 9, 93–112. <https://doi.org/10.2307/1447287>.
- Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 2196–2218. <https://doi.org/10.1139/f92-242>.
- Winemiller, K. O., Taphorn, D. C., & Barbarino-Duque, A. (1997). Ecology of *Cichla* (Cichlidae) in two blackwater rivers of southern Venezuela. *Copeia*, 1997, 690–696. <https://doi.org/10.2307/1447287>.
- Zaret, T. M. (1980). Life history and growth relationships of *Cichla ocellaris*, a predatory South American cichlid. *Biotropica*, 12, 144–157. <https://doi.org/10.2307/2387730>.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Soares Guedes GH, Gomes ID, Alves do Nascimento A, Silva de Aguiar F, Araújo FG Equilibrium reproductive strategy of the peacock bass *Cichla kelberi* facilitates invasion into a Neotropical reservoir. *J Fish Biol.* 2021;98:743–755. <https://doi.org/10.1111/jfb.14618>