Reproductive biology of seven fish species of commercial interest at the Ramsar site in the Baixada Maranhense, Legal Amazon, Brazil

Irayana Fernanda da Silva Carvalho[1], Lorrane Gabrielle Cantanhêde[2], Ana Luiza Caldas Diniz[1], Raimunda Nonata Fortes Carvalho-Neta[3] and Zafira da Silva de Almeida[3]

Correspondence:
Irayana Fernanda da Silva Carvalho
nanda.dih@live.com

The purpose of this study is to determine the parameters of the reproductive biology of seven commercial species at the Ramsar Site of the Baixada Maranhense to support fisheries management measures. The collections were carried out between 2012 and 2016. The reproductive period, sex ratio, weight–length relationship and first sexual maturity were evaluated for seven species of commercial importance. The sex ratio showed that females are predominant for all species, except for *Plagioscion squamossissimus*. The weight-length relationship indicated a greater investment in weight for *Cichla monoculus* and *Hassar affinis*, and a greater investment in length for *Hoplias malabaricus*, *Plagioscion squamosissimus*, *Prochilodus lacustris*, *Pygocentrus nattereri*, and *Schizodon dissimilis*. The reproductive activity of the species was predominant in the rainy season, but *C. monoculus*, *H. malabaricus* and *P. lacustris* showed the ability to reproduce in both seasons. As management measures for the region, it is suggested a change in the closed fishing season established by IBAMA, from December 1 to April 30, to ensure the protection of all commercial species in this study.

Keywords: Closed fishing season, Environmental Protection area, Fisheries Management, Freshwater Fish, Reproduction.

1 Programa de Pós-Graduação em Recursos Aquáticos e Pesca, Departamento de Química e Biologia, Universidade Estadual do Maranhão, Av. Lourenço Vieira da Silva, 1000, Jardim São Cristovão, 65055-310 São Luís, MA, Brazil. (IFSC) nanda.dih@live.com, (corresponding author); (ALCD) luizadiniz13@hotmail.com.

2 Programa de Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Pará/Museu Paraense Emílio Goeldi – UFPA/MPEG, Rua Augusto Corrêa, 01, Guamá, 66075-110 Belém, PA, Brazil. (LGC) lorranegabrielle@hotmail.com.

3 Departamento de Química e Biologia, Universidade Estadual do Maranhão, Av. Lourenço Vieira da Silva, 1000, Jardim São Cristovão, 65055-310 São Luís, MA, Brazil. (RNFCN) raifortes@gmail.com; (ZSA) zafiraalmeida@gmail.com.

Este estudo teve como objetivo determinar os parâmetros da biologia reprodutiva de sete espécies comerciais no Sítio Ramsar da Baixada Maranhense, para apoiar medidas de manejo pesqueiro. As coletas foram realizadas entre 2012 e 2016, com um ano de coleta para cada espécie. Foram avaliados o período reprodutivo, a razão sexual, a relação peso-comprimento e a primeira maturidade sexual para sete espécies de importância comercial. A razão sexual mostrou que as fêmeas são predominantes para todas as espécies, exceto para *Plagioscion squamossissimus*. A relação peso-comprimento indicou um maior investimento em peso para *Cichla monoculus* e *Hassar affinis*, e um maior investimento em comprimento para *Hoplias malabaricus*, *Plagioscion squamosissimus*, *Prochilodus lacustris*, *Pygocentrus nattereri* e *Schizodon dissimilis*. A atividade reprodutiva das espécies foi predominante na estação chuvosa, mas *C. monoculus*, *H. malabaricus* e *P. lacustris* mostraram capacidade de se reproduzir nas duas estações. Como medidas de manejo para a região, sugere-se uma mudança do período de defeso, estabelecida pelo IBAMA, de 1 de dezembro a 30 de abril, para garantir a proteção de todas as espécies comerciais.

Palavras-chave: Área de Proteção Ambiental, Gestão pesqueira, Peixes de água doce, Período de defeso, Reprodução.

INTRODUCTION

The growing number of studies on the reproductive biology of fish is the result of efforts to understand biological processes and the preservation of aquatic ecosystems to contribute to the productivity of fishing systems (Lowerre-Barbieri, 2009; Jakobsen *et al.*, 2016). Fishing systems where artisanal fishing is the main activity and that might become environments with low fish stocks require more and deeper studies (Lowerre-Barbieri *et al.*, 2011), especially in places where little is known about the fishery resources. This is the case of Brazil and its large number of rivers and artisanal fishing communities, as well as its large environmental Conservation Districts and protected areas used for fishing, mainly for subsistence purposes.

In Maranhão State, there are large protected areas of ecological and economic importance, three of which can be mentioned here for their relevance in fishing: the Baixada Maranhense, the Reentrancias Maranhenses, and a portion of the Manoel Luís Marine State Park. The Baixada Maranhense is located within the region known as the Legal Amazon, being predominantly *varzea* [floodplains] (Conceição *et al.*, 2013). Artisanal fishing is the main source of income and subsistence, and although it occurs on a small scale, it has negative impacts on local fish fauna.

The only fishing regulation particular to the region is Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) ordinance number 85/2003. The absence of fishing regulations and norms leads to overexploitation of fish stocks. Closed fishing season can allow the renewal and maintenance of fishing stocks, in efforts to ensure the sustainability of fishing (Ruffino, 2005). However, the implementation of closed fishing seasons must consider aspects such as reproductive periods and local

fishing activities. Thus, establishing periods when fishing is not permitted by law is necessary to preserve species, and is determined by the reproductive period of the the target species (Maia, 2009). Thus, studies that aim to verify if these objectives have been achieved are extremely relevant and can help improve strategies for the protection of environments and natural resources without impacting the traditional communities that depend directly on them.

Spawning is increasingly recognized as a component of the reproductive strategies of many species. These strategies can be modified by environmental conditions (Dala-Corte, Azevedo, 2010; Rideout, Tomkiewicz, 2011). It is also necessary to understand the dynamics of a fishing area and the perpetuation of certain species to support fisheries management. Therefore, studying the reproductive cycle of economically important species from the Baixada Maranhense is essential to understanding their population dynamics, and contribute to local fisheries management. The reproductive cycles of some economically important species in the Baixada Maranhense region have already been evaluated individually, such as *Hassar affinis* (Steindachner, 1881) (Cantanhêde *et al.*, 2016, 2017) and *Plagioscion squamosissimus* (Heckel, 1840) (Carvalho *et al.*, 2017). However, to evaluate reproductive parameters, such as sex ratio, weight-length relationship, reproductive periodicity, and spawning season of a group of economically important species is essential to determine closed fishing season and minimum catch sizes suitable for this region, because the legislation will be based on the reproductive characteristics of the species that suffer the greatest fishing pressure.

Therefore, the goal of this study was to determine the main parameters of reproductive biology in seven species with commercial importance that inhabit the Ramsar site in Brazil, by examining sex ratio, weight-length relationship, reproductive periodicity and spawning season, to verify: whether the closed fishing season established by IBAMA (Ordinance Nº 85/2003), which runs from December to March, covers all of the species in this study in relation to spawning seasons. Our hypothesis is that since rain is an important environmental factor for the reproduction of Amazonian species (Sánchez-Botero, Araújo-Lima, 2001; Leite *et al.*, 2006), the closed fishing season determined by IBAMA, which comprises months of the rainy season, will be suitable for these species.

MATERIAL AND METHODS

Study area. This study was carried out in the Baixada Maranhense Environmental Protection Area, which is a "Wetlands of International Importance" or Ramsar Site, designated by Brazil under the UN Convention on Wetlands, since the area has ecological, social, economic, cultural, scientific, and recreational importance (MMA, 2010; Ramsar Convention Secretariat, 2013). This region consists of a large ecological complex with many components, including rivers and lakes that support fishing in the region.

The data was acquired through the compilation of past data obtained during the REBAX project, between 2012 and 2016, in the Baixada Maranhense lake system (Cajari Lake, Viana Lake, Aquiri Lake, Itans Lake and Coqueiro Lake) influenced by the Pindaré and Mearim rivers (Fig. 1), which together form a drainage basin with water flowing into the Maranhense Gulf.
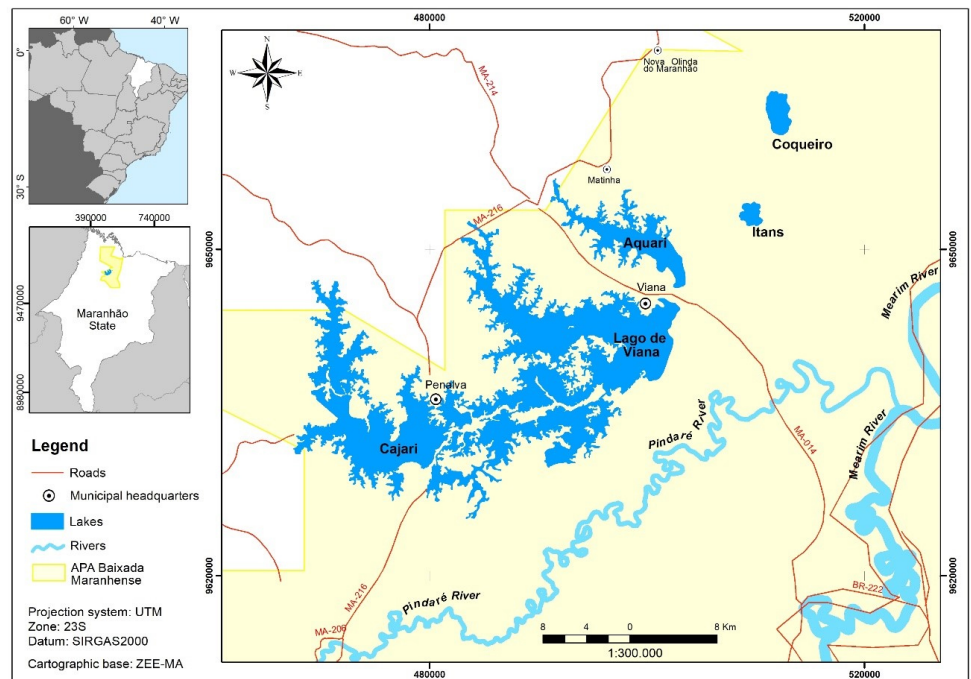
FIGURE 1 | Map of Baixada Maranhense Environmental Protection Area, a Brazilian Ramsar Site.

Data collection. The species examined in this study are part of the target species group in the region, which support the local economy. According to the last fishing bulletin issued by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio, 2011), these species are caught in large volumes by continental fisheries throughout Brazil: *Cichla monoculus* Spix & Agassiz, 1831 (Tucunaré – 9,304.4 t); *Hassar affinis* (Mandi – 6,479.9 t); *Hoplias malabaricus* (Bloch, 1794) (Traíra – 9,894.0 t); *Plagioscion squamosissimus* (Pescada – 13,150.3 t); *Prochilodus lacustris* Steindachner, 1907 (Curimatá – 28,643.0 t); *Pygocentrus nattereri* Kner, 1858 (Piranha – 3,672.8 t); *Schizodon dissimilis* (Garman, 1890) (Aracu – 5,211.3 t).

Each species was evaluated for one year, in monthly collections. The collection sites were chosen because they are lakes that are permanently flooded and have high importance for fishing activities, contributing to the high quantity of fish supplied by the state of Maranhão. According to the last fishery production report issued by the ICMBio (2011), Maranhão produces approximately 26,000 tons of fish per year, which supplies the state itself and other regions of Brazil (Costa-Neto *et al.*, 2001; Piorski *et al.*, 2005; ICMBio, 2011).

The specimens were obtained through experimental and commercial fishing at the local port to complement the sampling by size class. Two fishing nets of different lengths and meshes were used. The first net was 800 m long with 4 cm between opposing nodes and the second fishing net was 1000 m long with 8 cm between opposing nodes. The nets were set in the late afternoon, remaining for 8 to 12 h, preferably during twilight periods.

After collection, the specimens were kept in ice and transported for analysis at the Fisheries and Aquatic Ecology Laboratory – LabPEA of the Universidade Estadual do

Maranhão (UEMA). Species identification was conducted by specialists and confirmed by molecular data. The voucher specimens were deposited at the Coleção de tecidos e DNA da fauna maranhense (COFAUMA), at the UEMA – in São Luís, MA, Brazil. The voucher numbers for the seven species studied are shown in Tab. **S1**.

For each specimen collected, the following measurements were taken: total length (TL) in centimeters, measured between the ends of the mouth and the caudal fin, and total weight (TW) in grams. The macro- and microscopical analyses of the gonads sought to identify the sex and gonadal maturation stages, using the terminology proposed by Brown-Peterson *et al.* (2011) and Lowerre-Barbieri *et al.* (2011) with the following developmental phases: 'Immature (IP)' for fish that have never spawned, 'Developing (DP)' for fish with ovaries beginning to develop, but not ready to spawn, 'Spawning capable (SP)' for fish that are developmentally and physiologically able to spawn in this cycle, 'Regression (RP)' for those no longer spawning, and 'Regeneration (RGP)' for sexually mature fish, but reproductively inactive. All of the virgin individuals belong to phase IP, while all individuals in the other phases are considered adults. For histology, the gonads of some specimens were fixed in Bouin fluid, embedded in paraffin, stained with haematoxylin-eosin and examined under a light microscope.

The rainfall data were obtained from the "Programa de Monitoramento Climático em Tempo Real da Região Nordeste" (PROCLIMA, http://proclima.cptec.inpe.br/).

Data analysis. The weight–length relationship was established using non-linear regression. The adjustment of the curve represented by the mathematical expression $TW = a \times TL^b$, was obtained by the least squares method suggested by Zar (2010), where TW is the total weight of the fish, a is the linear regression coefficient, TL is the total length of fish and b is the slope of regression. We used Student's t-test to determine whether b values are significantly different from 3.0. These analyses were run in the nls and t.test functions of the *stats* package, in the R software (R Development Core Team, 2016).

The sex ratio was calculated for the total period and also for individual months. The sex ratios obtained were tested by the χ^2 (Chi-squared test) with a significance level of 5% to verify whether there was significant difference with the hypothesis of 1:1. This analysis was run in the chisq.test function of the *stats* package, in the R software.

Regarding the size at first sexual maturity (L_{50}), gonadal maturation stages were grouped into immature (stage IP) and mature stages (stages DP+SP+RP+RGP), according to Vazzoler (1996) and Ortiz-Ordónez *et al.* (2007), using terminology for gonadal maturation stages suggested by Brown-Peterson *et al.* (2011) and Lowerre-Barbieri *et al.* (2011). The percentage of adult specimens by length class was calculated and considered as a dependent variable and the total length as an independent variable. Subsequently, these values were adjusted to a logistical curve using the Statistica software, version 7.0, under license from the Laboratory of Fisheries and Aquatic Ecology (UEMA), according to the formula: $P = 1 / (1 + \exp [- r (TL - L_{50})])$, where: P = proportion of mature individuals; r = slope of the curve; TL = total length; L_{50} = size of first sexual maturity.

The determination of the periodicity of the reproductive cycle was based on the frequency of gonadal maturation stages, and on the variation of the mean values of the gonadosomatic index (?GSI) (Vazzoler, 1996). The gonadosomatic index is the

difference between GSI_1 and GSI_2, given by the equations:

$$GSI_1 = \frac{GW}{TW} \times 100$$

$$GSI_2 = \frac{GW}{CW} \times 100$$

where: GW = gonad weight; TW = total weight of the individual; CW = TW–GW.

The gonadosomatic index defines the percentage that the gonad represents of the animal's total weight and is indicative of variations in gonadal development during the year. The higher values of GSI are indicative of the advanced maturation and mature stages of gonadal development.

A significance level of 0.05 was used in all tests, and all analyses were performed using Microsoft® Excel version 16.0 with the Action Stat supplement.

RESULTS

We analyzed 3,217 fish specimens, including 1,180 males and 2,037 females. *Hoplias malabaricus* was the most predominant species. The smallest species captured was *H. affinis*, which ranged from 10 cm to 21 cm. The species with the highest weight was *C. monoculus*, which ranged from 40 g to 2,000 g.

Weight–length relationship. The species *P. lacustris*, *S. dissimilis* and females of *H. malabaricus* and *P. squamosissimus* had negative allometry, with greater growth in length than weight. While *C. monoculus*, *H. affinis*, *P. nattereri,* and males of *H. malabaricus* and *P. squamosissimus* had positive allometry, with greater investment in weight than length (Tab. 1).

Sex ratio. The sex ratio for each species shows that females of all species are predominant in the study region, except for *P. squamosissimus* (Tab. 2). Females of *H. malabaricus* accounted for 81.8% of the local catches. For all species, the percentage of males and females decreases in the larger size classes (Fig. 2; see sample size by length class in Tab. **S2**). Females were predominant over males in practically every month for the seven species (Fig. 3).

First sexual maturity. For *H. malabaricus*, *P. squamosissimus*, *P. lacustris*, *P. nattereri,* and *S. dissimilis* (Figs. 2C–G), the pattern observed regarding the distribution of the absolute frequency of gonadal maturation stages showed that these species reproduce early, since adult individuals were found in the smaller length intervals. The species *C. monoculus* and *H. affinis* did not show this pattern. The comparison between size at first sexual maturity (L_{50}) and the maximum length reached by individuals also reinforces this finding (Tab. 3).

TABLE 1 | Weight-length relationship parameters for males and females by species caught in Baixada Maranhense Protection Area, Legal Amazon, between January 2012 and December 2016. TW = Total weight; TL = Total length; a = the linear regression coefficient; b = slope of regression; CI = Confidence intervals; r^2 = Coefficient of determination. Asterisks indicate that B-values are significantly different from 3, using Student's T statistic with p < 0.05.

Species	Males								Females						
	N	TW(g)	TL(cm)	a (95% CI)	b (95% CI)	r^2	T- and *P*-value	N	TW(g)	TL(cm)	a (95% CI)	b (95% CI)	r^2	T- and *P*-value
Cichla monoculus	187	40–1,000	14.5–395	0.014 (0.011–0.018)	3.025 (2.952–3.099)	0.96	t= 81.68 (p<0.05)*	285	50–970	15–37.5	0.008 (0.006–0.011)	3.182 (3.107–3.258)	0.96	t= 84.81 (p<0.05)*
Hassar affinis	160	14.7–79.5	10.5–16.5	0.004 (0.002–0.007)	3.462 (3.235–3.692)	0.88	t= 30.36 (p<0.05)*	261	16.2–134.4	10.3–21	0.005 (0.004–0.007)	3.341 (3.217–3.465)	0.88	t= 52.40 (p<0.05)*
Hoplias malabaricus	126	50–480	15–32	0.008 (0.004–0.014)	3.104 (2.927–3.284)	0.89	t= 34.97 (p<0.05)*	541	20–540	12.7–37.5	0.012 (0.010–0.016)	2.976 (2.905–3.048)	0.81	t= 82.29 (p<0.05)*
Plagioscion squamosissimus	213	38.5–800	11.5–39.7	0.008 (0.006–0.011)	3.096 (3.009–3.183)	0.89	t= 71.54 (p<0.05)*	215	17.1–720	15.5–38	0.012 (0.008–0.020)	2.974 (2.832–3.116)	0.85	t= 41.70 (p<0.05)*
Prochilodus lacustris	149	32.5–208.5	12.5–22.2	0.030 (0.018–0.050)	2.818 (2.645–2.992)	0.88	t= 32.15 (p<0.05)*	198	6.8–210.3	12.5–22.8	0.034 (0.021–0.054)	2.778 (2.611–2.945)	0.74	t= 32.43 (p<0.05)*
Pygocentrus nattereri	189	11.7–304.5	11–21.6	0.027 (0.016–0.046)	3.022 (2.836–3.209)	0.71	t= 32.21 (p<0.05)*	236	50–308.2	11.5–21.3	0.028 (0.017–0.047)	3.011 (2.834–3.188)	0.81	t= 33.70 (p<0.05)*
Schizodon dissimilis	156	48.1–261	16.4–31.9	0.156 (0.083–0.294)	2.164 (1.967–2.362)	0.77	t= 21.18 (p<0.05)*	301	50–484.2	16.3–38.5	0.040 (0.030–0.053)	2.594 (2.505–2.682)	0.88	t= 56.86 (p<0.05)*

TABLE 2 | Sex ratio between males and females by species caught in Baixada Maranhense Protection Area, Legal Amazon, between January 2012 and December 2016. Asterisks indicate statistical significance in sex ratio, as determined by Chi-square test (p < 0.05).

| Species	N	Males	%	Females	%	Sex Ratio	x^2	P
Cichla monoculus	472	187	39.6	285	60.3	1.5F:1M	20.34	<0.05*
Hassar affinis	421	160	38.0	261	61.9	1.6F:1M	24.23	<0.05*
Hoplias malabaricus	667	126	19.0	541	81.8	4.2F:1M	258.2	<0.05*
Plagioscion squamosissimus	428	213	49.7	215	50.2	1.0F:1M	0.009	0.92
Prochilodus lacustris	328	142	43.2	186	56.7	1.3F:1M	6.91	0.008*
Pygocentrus nattereri	425	189	44.4	236	55.5	1.2F:1M	5.19	0.022*
Schizodon dissimilis	457	156	34.1	301	65.8	1.9F:1M	46.00	<0.05*
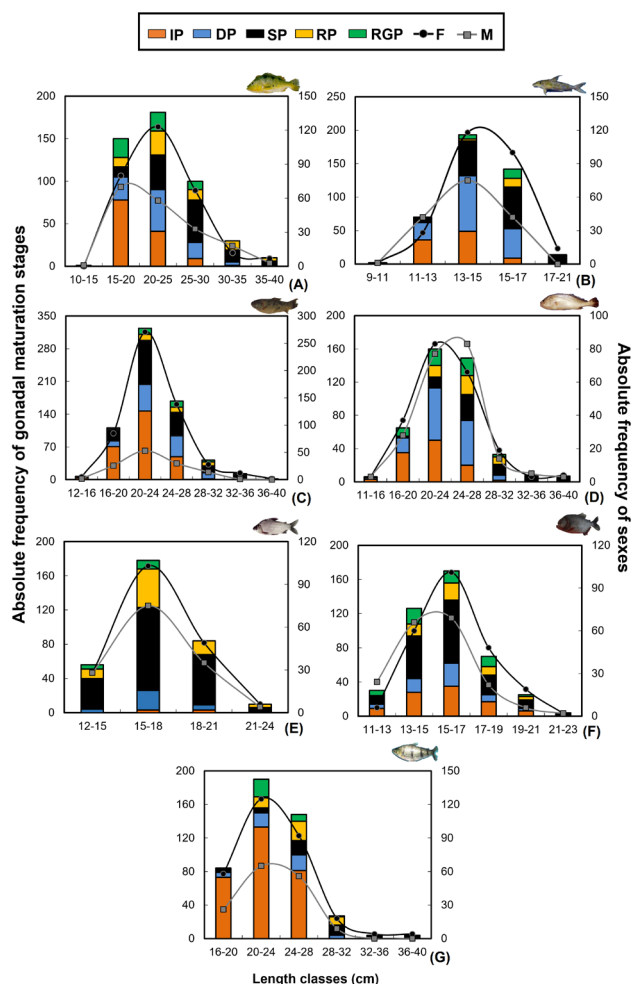
FIGURE 2 | Distribution of the relative frequency by length classes, gonadal maturation stages, and sexes: (A) *Cichla monoculus*; (B) *Hassar affinis*; (C) *Hoplias malabaricus*; (D) *Plagioscion squamosissimus*; (E) *Prochilodus lacustris*; (F) *Pygocentrus nattereri*; and (G) *Schizodon dissimilis*, caught in Baixada Maranhense Protection Area, between January 2012 and December 2016. Immature (IP); Developing phase (DP); Spawning capable (SP); Regression (RP); Regeneration (RGP), F (Female) and M (Males).
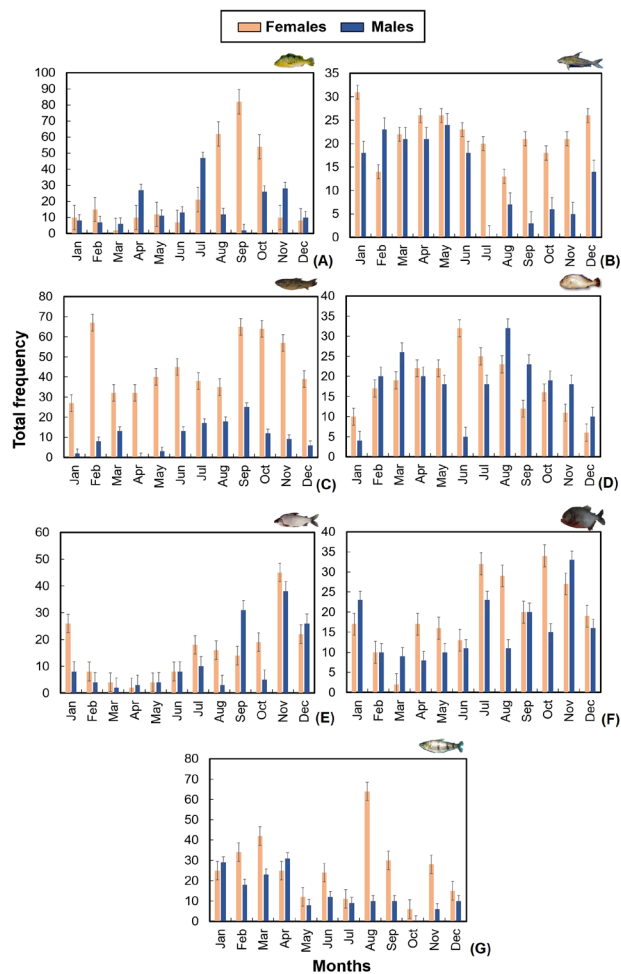
FIGURE 3 | Distribution of the relative frequency of males and females by collection months: (A) *Cichla monoculus*; (B) *Hassar affinis*; (C) *Hoplias malabaricus*; (D) *Plagioscion squamosissimus*; (E) *Prochilodus lacustris*; (F) *Pygocentrus nattereri*; and (G) *Schizodon dissimilis*, caught in Baixada Maranhense Protection Area, between January 2012 and December 2016.

TABLE 3 | Size at first sexual maturity (L_{50}) for seven species captured in the Baixada Maranhense caught from January 2012 to December 2016.

Species	Length range (cm)	Length at first maturity (L_{50}, cm)
Cichla monoculus	14.5–39.5	16.8
Hassar affinis	10.3–21	12.3
Hoplias malabaricus	12.7–37.5	19.0
Plagioscion squamosissimus	11.5–39.7	17.3
Prochilodus lacustris	12.5–22.8	14.4
Pygocentrus nattereri	11–21.6	14.3
Schizodon dissimilis	16.3–38.5	25.0

Reproductive period. Based on the gonadosomatic index for *C. monoculus*, *H. affinis*, *H. malabaricus*, *P. squamosissimus*, *P. lacustris*, *P. nattereri,* and *S. dissimilis*, we observed that the reproductive period of all the species coincides with the rainy season (Fig. 4). When grouping the reproductive periods of the species up to the spawning peak, it is possible to notice that the closed fishing season suggested by IBAMA (Ordinance N° 85/2003) is adequate (December to March) for these species.

The species *Cichla monoculus*, *Hassar affinis* and *Schizodon dissimilis* showed spawning periods during the rainy season, with peaks in the intervals from January to March, March to May and December to February, respectively. The species *Hoplias malabaricus*, *Plagioscion squamosissimus*, *Prochilodus lacustris,* and *Pygocentrus nattereri* presented spawning periods in both the dry and rainy seasons. However, spawning peaks occurred during the rainy season, in the intervals from January to March for the first three and in December and January for *P. nattereri* (Fig. 5).
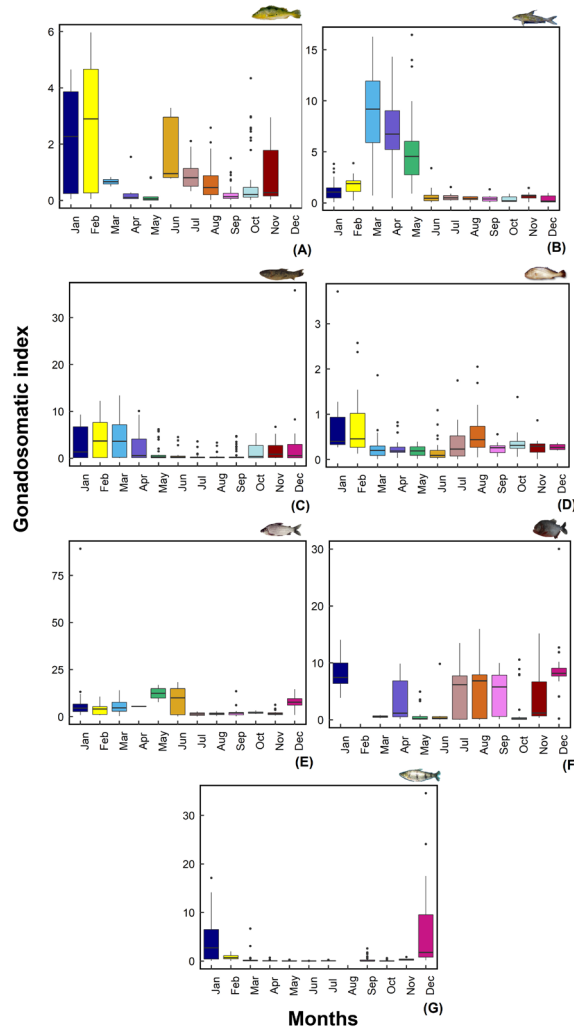

FIGURE 4 | Gonadosomatic index indicating the spawning season for (**A**) *Cichla monoculus*; (**B**) *Hassar affinis*; (**C**) *Hoplias malabaricus*; (**D**) *Plagioscion squamosissimus*; (**E**) *Prochilodus lacustris*; (**F**) *Pygocentrus nattereri*; and (**G**) *Schizodon dissimilis*, caught in Baixada Maranhense Protection Area, between January 2012 and December 2016.
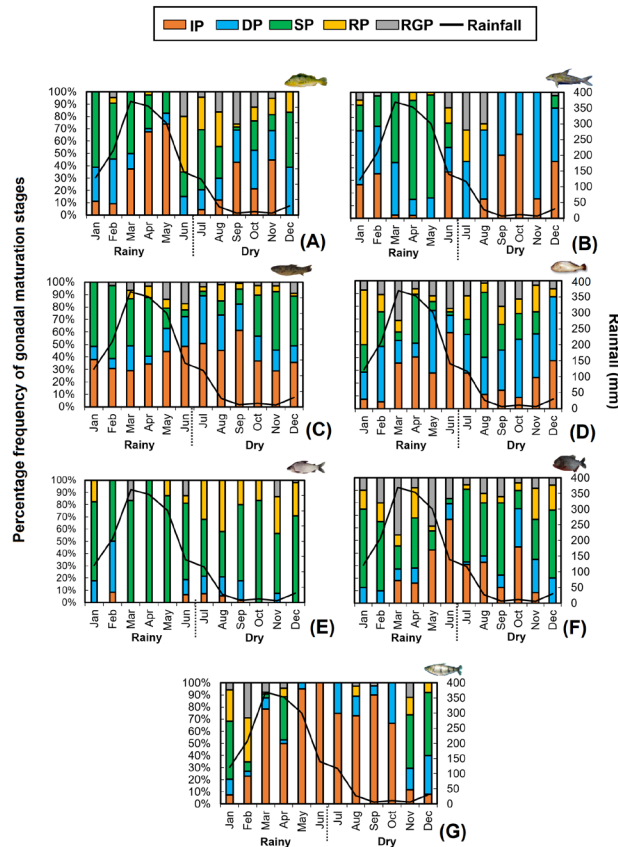
FIGURE 5 | Relative frequency of gonadal maturation stages during the rainy and dry seasons. (**A**) *Cichla monoculus*; (**B**) *Hassar affinis*; (**C**) *Hoplias malabaricus*; (**D**) *Plagioscion squamosissimus*; (**E**) *Prochilodus lacustris*; (**F**) *Pygocentrus nattereri*; and **G**. *Schizodon dissimilis*, caught in Baixada Maranhense Protection Area, between January 2012 and December 2016. Immature (IP); Developing phase (DP); Spawning capable (SP); Regression (RP); Regeneration (RGP), F (Female) and M (Males).

DISCUSSION

Our results demonstrate that the reproductive period of all the species occurs during the rainy season, corroborating with the period established by the current legislation for the region. However, there is an instability between the dry and rainy periods in the region, and the seasons are not always well defined, varying over the years, with shorter and longer dry periods, or longer rainy periods and shorter droughts, which is not foreseen by the legislation. Therefore, there is a need to revise the closed fishing season to account for a wider reproductive range among the commercial species of this study. Since, three species (*H. affinis*, *P. lacustris*, and *P. nattereri*) showed reproductive peaks in April and/or May, they are not protected by the current closed fishing season, which runs from December to March, justifying the extension.

The frequency of gonadal maturation stages and length at first sexual maturity, indicate that the species in this region enter their reproductive phases with reduced lengths in relation to the maximum lengths observed. On the other hand, we found that the study area has excellent conditions for feeding, growth and spawning, confirmed by

the presence of all gonadal maturation stages during the study period. This information is a tool to promote fisheries planning through management policies for this Ramsar Site, which is a wetlands that provides fundamental ecological services, in addition to being a source of biodiversity at all levels, and thus requires protection and sustainable use of its natural resources.

Reproduction and growth are production processes that compete for the same limited resources. All energy obtained from food is stored in the body and used in the synthesis of tissues and during metabolic processes (Calow, 1985). During the juvenile phase, all allocated energy is used for linear growth and the development of somatic structures, triggering the investment in length in fish, characterizing negative allometry. During adulthood, all allocated energy is designated for the development of reproductive structures and for the storage of energy reserves that will be used during maturation and spawning, which characterizes investment in body weight, that is, positive allometry. Thus, allometric variations occur according to the availability of resources and the life stages of fish (Vazzoler, 1996).

As for the weight-length relationship, it is observed that there is a greater investment in weight than in length for *H. affinis*. This result provides relevant information about the consequences of human actions in the region, such as the damming of water sources (Agostinho *et al.*, 2007). Cantanhede *et al.* (2016) performed this same analysis for *H. affinis*, in only one of the Baixada Maranhense lakes and found negative allometry. According to these authors, the species usually migrates between the Lakes of Viana, Aquiri and Penalva, all belonging to the lake system evaluated in our study. However, the presence of dams between these lakes prevents the movement of fish to other areas, especially when the water level decreases during the dry season, limiting resources in this period. Consequently, the portion of energy destined for their reproduction is catalyzed during the period of limited resources, affecting their reproductive strategies, starting with maturation and metabolic transformations (Montenegro *et al.*, 2011; Resende, Gondolo, 2017; Lima *et al.*, 2017). Therefore, investing in weight allows *H. affinis* to resist constant environmental changes, optimizing physiological activities (Froese, 2006).

The absence of natural predators of *C. monoculus* is a factor that influences its pattern of mass and energy gain, since this species was introduced accidentally in the studied environment. The differences between its natural environment and the environment in which a species is introduced can directly influence growth dynamics. Introduced peacocks bass tend to have a higher weight-length ratio compared to native populations due to intense predation and competition (Zaret, 1980; Ricciardi, MacIsaac, 2011; Taabu-Munyaho *et al.*, 2016) favoring positive allometry, as seen for this species in this study. Gomiero, Braga (2003), observed the same growth pattern for *C. monoculus* introduced in a Brazilian reservoir.

The distribution of the frequency of gonadal maturation stages and the size of first sexual maturity of *H. malabaricus*, *P. squamosissimus*, *P. lacustris*, *P. nattereri*, and *S. dissimilis*, revealed individuals classified as adults in the smaller length classes. The presence of adults in the smaller classes can be due to several factors, such as capture pressure (Cantanhêde *et al.*, 2017), habitat change due to human interference (Pankhurst, Munday, 2011), introduction of exotic species (Kiruba-Sankar *et al.*, 2018), competition or a predation effect (Creel, Chritianson, 2008). These factors alone or together may be accelerating

the reproductive development of these species, resulting in early maturation in smaller sizes. A gradual development pattern of gonadal maturation stages is observed regarding the length sizes for *C. monuculus* and *H. affinis*. In the smaller length classes, there are only immature juvenile individuals, with the other reproductive phases developing as the intervals of length classes increase.

The species investigated in this study are classified as target species in the region, as they are important for the local economy. Due to their importance, the local fishing effort is strongly concentrated on them (Silva, 2015), which is reflected in the higher number of females in the catches. This may be a problem for the maintenance of the stocks of each species, since selective fishing usually negatively affects larger individuals (Conover, Munch, 2002). Females are included in this group because they are larger, mainly during reproductive periods due to the increase of body size when gonads are mature. The higher capture of females in the medium and long-term will harm the fishing sector, since it will affect reproductive rates and be reflected in the maintenance of stocks.

Sex ratios in fish populations are as close as possible to 1:1 (Vazzoler, 1996; Andrade *et al.*, 2015), maintaining the balance in their stocks. The results related to the sexual proportion associated with the length classes and gonadal maturation stages showed that the species may have been caught before the end of their breeding periods. Thus, it is necessary to implement management systems to maintain reproductive activities, favoring the maintenance of balanced sex ratios. Froese *et al.* (2016) suggests three rules for the proper functioning of a fisheries management system, two of which may apply to this situation. The first rule states that mortality from fisheries should be less than the natural rate of mortality of the fish in the environment, and to achieve this, humans should fish less than nature can compensate for through reproduction. The second rule would be to maintain population sizes above 50 percent of natural abundance, to attain levels at which fish populations are able to perform their ecological functions either as prey or predator.

IBAMA ordinance 85/2003 prohibits fishing from December 1 to March 30 each year , in watersheds, streams, lakes, reservoirs and public dams (IBAMA, 2003) in the state of Maranhão. This period coincides with the rainy season in the Baixada Maranhense region (January to June) (Costa-Neto *et al.*, 2001) and covers at least one spawning season for all of the species studied here. However, we suggest that future studies evaluate the possibility to extend the closed fishing season to five months. With a longer closed fishing season, fishing activities would be reduced, and they could receive financial support from the government for a longer period and conduct secondary subsistence activities. On the other hand, fish can reproduce during most of the rainy season, ensuring the maintenance of stocks. Therefore, there would be better conditions for survival of the juveniles, due to the greater availability of food and a greater number of proper spawning habitats (Junk *et al.*, 1989; Röpke *et al.*, 2016; Barthem *et al.*, 2017).

Although *H. affinis* and *P. squamosissimus* are also commercially exploited along with the other species, both have biannual spawning seasons. For this reason, it would be ideal to establish more than one closed fishing season per year for these two species. According to current Brazilian law and considering the difficulties for the fishermen to distinguish more than one closed fishing season during the year and to return the species to the environment, a five-month period is suggested. It should be emphasized

that within this recommendation, only the reproductive period of *H. affinis* and *P. squamosissimus* would be protected, and the possibility of applying specific management measures for these species should not be ruled out.

A closed fishing season is the first step for the protection of a species during its breeding season, and a tool for promoting the responsible use of natural resources. Therefore, it is necessary to extend this study to the other watersheds located in Maranhão to identify the adequate closed fishing season for other commercial species, or the implementation of fishing legislation for the Baixada Maranhense Environmental Protection Area, considering the local ecological patterns.

Fish reproduction and development are closely linked to flood periods, particularly in tropical floodplain systems (Santos *et al.*, 2010; Braga *et al.*, 2012). Flood periods are highly predictable in the study region. After the dry season, with the arrival of the rains, the reproductive activities begin, which is important for the reestablishment of the fish populations (Agostinho *et al.*, 2004). The arrival of the rains controls the pulse of flooding in the Baixada Maranhense lake system. During this period, the ecological processes and patterns that drive the habitat dynamics are established, modifying feeding and growth areas, triggering reproductive processes and indicating the right time for fish spawning (Correa, Winemiller, 2014; Mortillaro *et al.*, 2015; Prudente *et al.*, 2016). The rainy season has already been reported in other studies carried out in the region as a period of reproductive activity for *H. affinis*, *P. squamosissimus,* and *P. lacustris* (Cantanhêde *et al.*, 2016; Carvalho *et al.*, 2017; Cardoso *et al.*, 2019), corroborating with this study.

The fact that *C. monuculus*, *H. affinis*, *H. malabaricus*, *P. squamosissimus*, *P. lacustris*, *P. nattereri,* and *S. dissimilis* prefer the rainy season for spawning (Cantanhêde *et al.*, 2016; Carvalho *et al.*, 2017; Cardoso *et al.*, 2019) is related to the survival conditions of their larvae and juveniles. During the rainy season, dispersion is facilitated by flooding, with less risk of predation and competition for resources (Patrick, 2016). In addition, the vegetation, stones and tree trunks on the lakesides during the dry season, become refuges and sources of food for juveniles during the rainy season (Sánchez-Botero, Araújo-Lima, 2001; Leite *et al.*, 2006).

The strong selection of the most important commercial species (Mendonça, Pereira, 2013) negatively affects the maintenance of stocks, so that, in the next reproductive cycles, they must use reproductive strategies that favor survival (Araújo *et al.*, 2012; Chellappa *et al.*, 2013; Barros *et al.*, 2016), such as early maturation and changes in their growth patterns. Anthropogenic pressures also affect spatio-temporal dynamics. For example, the presence of dams between lakes affects the water courses that the fish use for reproduction, and with the onset of drought, river and lake levels fall, and fish cannot return to their places of origin (Fonteles Filho, 2011; Mims, Olden, 2013; Carvalho *et al.*, 2017). This mechanism leads to an increase in the capture rates of females, since they will be available longer, searching for food to store and recover energy before and after reproduction, respectively.

In addition, seasonal changes in the Baixada Maranhense are responsible not only for the reproductive adaptations of the fish, but also for the work dynamics of local fishermen. When fish are scarce, fishing efforts are increased to raise the catch. This intensification of fishing activities is triggered by the seasonal reduction of the flooded area that occurs annually (Lowe-McConnell, 1999; Montenegro *et al.*, 2013; Carvalho *et al.*, 2017) which also controls the flood pulse.

This is the first study to group seven commercial species that inhabit the Baixada Maranhense Environmental Protection Area. Cantanhêde *et al.* (2016), Carvalho *et al.* (2017), and Cardoso *et al.* (2019) carried out the first studies on the reproduction of fish in the region. Since these studies are recent, they focus on the need to adopt management measures to maintain the fish stocks of the species studied. The lack of studies on these species hinders the comparison and monitoring of the development of their reproductive cycles, especially in terms of their spawning season.

The lack of historical data on fishing in the Baixada Maranhense region makes it difficult to compare the populations of the species investigated here. Studies on the population dynamics in the region, analysis of CPUE to identify the decrease of the catches in a temporal series, as well as studies that report the influence of the constant habitat changes in the region due to the flood pulse must be the basis for fisheries management policies for this Environmental Protection Area. This study provides valuable information for reinforcing the validity of the current closed fishing season law, but it should be used with caution, as other species found in the region have not been evaluated here. For this reason, we reaffirm the need for further studies on the food and reproductive ecology of other fish species in the Baixada Maranhense, to allow implementing more comprehensive laws.

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AUTHOR'S CONTRIBUTION ⬤

Irayana Fernanda da Silva Carvalho: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review and editing.

Lorrane Gabrielle Cantanhêde: Conceptualization, Data curation, Formal analysis, Investigation, Writing-original draft, Writing-review and editing.

Ana Luiza Caldas Diniz: Conceptualization, Data curation, Formal analysis, Investigation, Writing-review and editing.

Raimunda Nonata Fortes Carvalho–Neta: Funding acquisition, Project administration, Resources, Supervision, Writing-original draft, Writing-review and editing.

Zafira da Silva de Almeida: Data curation, Funding acquisition, Project administration, Resources, Supervision, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

The fishes samples received from commercial catches in the Maranhão were dead, thus, this part of the collection did not involve animal experimentation or harm. The fishes samples received from experimental catches complied with Brazil animal welfare laws, guidelines and policies as approved by SISBIO license number 32.643.

COMPETING INTERESTS

The authors declare no competing interests.

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