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Feeding and reproductive ecology of *Cichla piquiti* Kullander & Ferreira, 2006 within its native range, Lajeado reservoir, rio Tocantins basin

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Cichla piquiti is endemic to the Tocantins-Araguaia river basin, but information about its biology is restricted to populations introduced in other basins. In order to fill this gap, we investigated the feeding ecology and reproductive dynamics of *C. piquiti* in Lajeado reservoir, rio Tocantins. A total of 270 fish were collected between November 2010 and October 2011. The diet is rich and composed of at least 23 resources, predominantly fish (at least 19 species). We observed no clear influence of sex, periods and ontogeny on diet, which was basically composed of Characidae and Cichlidae. Considering its reproductive dynamics, immature, reproductive and non-reproductive fish were recorded during the whole study, and reproductive effort did not differ among periods. *Cichla piquiti* also showed no pattern of energy allocation between reproductive and somatic activities. These results indicate that reproduction is occurring throughout the year and that this activity is not synchronized among individuals. In conclusion, this study presented valuable information on the ecology of *C. piquiti* within its natural range, which may subsidize management programs to conserve local stocks. This information may also provide theoretical insights to explain why *C. piquiti*, a voracious predator, is so harmful when introduced in non-Amazonian reservoirs.

Cichla piquiti é uma espécie endêmica da bacia Tocantins-Araguaia, porém o conhecimento sobre sua biologia está amparado no estudo de populações introduzidas em outras bacias. Para preencher essa lacuna, o presente estudo investigou a ecologia alimentar e reprodutiva de *C. piquiti* no reservatório de Lajeado, rio Tocantins. Um total de 270 peixes foi coletado entre novembro/2010 e outubro/2011, na região superior do reservatório. A dieta da espécie é rica e envolveu a ingestão de pelo menos 23 recursos, com predomínio de peixes (pelo menos 19 espécies). Não observamos padrão de variação na dieta entre os sexos, períodos e ontogenia, com predomínio no consumo de Characidae e Cichlidae. Considerando a dinâmica reprodutiva, peixes imaturos, em reprodução e repouso foram registrados ao longo do ano, e o esforço reprodutivo (IGS) não diferiu entre os períodos. *Cichla piquiti* também não apresentou padrão claro de alocação de energia entre atividades somáticas e reprodutivas. Esses resultados indicam que a reprodução ocorre durante todo o ano e que essa atividade não é sincronizada entre os indivíduos. Concluindo, o presente estudo apresentou informações importantes sobre a ecologia de *C. piquiti* em sua área de distribuição natural, que devem embasar programas de manejo para a conservação dos estoques na região. Essas informações devem também fornecer suporte teórico para explicar porque *C. piquiti*, um predador voraz, é tão danoso quando introduzido em reservatórios não-Amazônicos.

Keywords: Diet, Management, Population, Predator, Recruitment.

Introduction

Large impoundments modify permanently the physical and chemical structure of river systems and cause profound changes in the structure of fish populations (Agostinho *et al.*, 2008). Species that have pre-adaptations to complete their life cycle (*e.g.*, feeding, reproduction and growth) in the reservoir acquire biological relevance and can dominate fish assemblages (Agostinho *et al.*, 2007; Araújo *et al.*, 2013). Some non-migratory species, in particular, play a central role in structuring new assemblages, playing important ecological functions in the reservoir (Hoeinghaus *et al.*, 2009). This is the case of peacock-bass species (*Cichla*), which have successfully colonized many Neotropical reservoirs. These fishes are native to the Amazon basin, and, under natural conditions, are found in littoral habitats of rivers and lakes where they feed upon small-sized fish (Jepsen *et al.*, 1997; Winemiller, 2001; Hoeinghaus *et al.*, 2003). In reservoirs, *Cichla* finds suitable habitats for feeding and breeding, considering that prey fish are abundant (Pelicice *et al.*, 2005; Luz-Agostinho *et al.*, 2006) and shallow areas provide shelter and nesting sites. In fact,

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Cichla has colonized and spread in reservoirs where it is native (Santos & Oliveira Junior, 1999; Camargo & Petrere Jr., 2004) and non-native (*e.g.*, Gomiero *et al*., 2009; Pelicice & Agostinho, 2009; Espínola *et al*., 2010; Luiz *et al*., 2011).

Although *Cichla* species are native to the Amazon basin, few studies have been conducted in Amazonian reservoirs (*e.g.*, Novaes *et al*., 2004; Freire & Freitas, 2013). Basic ecological aspects (*e.g.*, feeding, reproduction) have been studied in hydrographic basins where *Cichla* is non-native, particularly in the rio Paraná basin (*e.g.*, Fugi *et al*., 2008; Souza *et al*., 2008; Gomiero *et al*., 2009; Pelicice & Agostinho, 2009; Vieira *et al*., 2009; Espínola *et al*., 2010; Villares Junior & Gomiero, 2010; Luiz *et al*., 2011; Santos *et al*., 2011). This information is important to clarify issues related to impact and invasion, but has little significance for the understanding of colonization, dynamics and persistence of native populations in Amazonian reservoirs. In this latter case, *Cichla* is a native species responding to novel environmental conditions, *i.e.* new feeding and reproduction opportunities created by the impoundment. For example, in natural fluvial environments, reproduction is usually constrained by water level variation (Jepsen *et al*., 1999; Muñoz *et al*., 2006), while feeding is diverse and essentially piscivorous (Jepsen *et al.,* 1997; Winemiller, 2001; Montaña *et al*., 2011). In non-Amazonian reservoirs, reproduction is constrained by temperature (Souza *et al*., 2008; Gomiero *et al*., 2009; Vieira *et al*., 2009; Pelicice *et al*., 2015) and diet is poor and based on cannibalism, invertebrates and non-native fish (Fugi *et al.,* 2008; Capra & Benneman, 2009; Villares Junior & Gomiero, 2010; Santos *et al*., 2011). In Amazonian reservoirs, however, feeding and breeding patterns may be less constrained by environmental variation, considering that seasonal variations in hydrology and temperature are small, and that prey fish (small-sized) are abundant and diverse. *Cichla* populations, under this scenario, may show long reproductive periods (Jepsen *et al*., 1999) and coexist with a diverse and abundant food supply. Therefore, studies conducted in Amazonian reservoirs are essential to understand how these native populations interact with the impoundment and successfully colonize lentic environments. In addition, this information is needed to manage and conserve viable populations in Amazonian reservoirs, especially because these fish acquire economic relevance and are targeted by artisanal, commercial and sport fisheries.

In this context, we investigated ecological aspects of *Cichla piquiti* in Lajeado reservoir (UHE Luis Eduardo Magalhães), rio Tocantins. *Cichla piquiti* is endemic to the Araguaia-Tocantins basin (Kullander & Ferreira, 2006), but it has been introduced in reservoirs elsewhere (Vieira *et al*., 2009; Luiz *et al*., 2011). In the area affected by Lajeado reservoir, the species is now economically relevant and have replaced large migratory species in markets. Thus, in order to understand the structure and dynamics of populations of *C. piquiti* in this reservoir, we investigated (i) patterns in feeding ecology (*i.e.* feeding activity, resources consumed and diet variation), (ii) reproductive dynamics (*i.e.* effort, period, length at first maturity) and (iii) temporal tradeoffs in the allocation of energy between somatic and reproductive activities. Differing from patterns observed in non-Amazonian basins, we expect that *C. piquiti* shows a diverse but essentially piscivorous diet, because small-sized fish dominate over littoral areas of the reservoir (F. M. Pelicice, *pers. obs*.). We also expect that *C. piquiti* reproduces all over the year, because water level variation in Lajeado reservoir is minimal and climate is tropical warm.

Material and methods

Study area. The rio Tocantins, together with the rio Araguaia, forms the Tocantins river basin, draining approximately 760,000 km^2 of central/north Brazil. This river extends through 2,500 km, discharging in the right bank of the lower Amazon. At present, the main channel is regulated by seven large dams, which stabilized the water level and changed the natural flow regime. The present study was carried out in the area affected by Lajeado reservoir (Luis Eduardo Magalhães Hydroelectric Plant; 902.5 MW installed capacity), located in the middle/upper portion of the basin. Closed in October 2001, the dam formed a reservoir with 630 km^2, 180 km long, 8.8 m mean depth (35 m near the dam), water residence time of 24 days and surface flow of 0.083 m/s (Agostinho *et al.*, 2011). Water level in the reservoir is stabilized and seasonal variation is minimal (< 1 m; www.edp.com.br, accessed April 2015).

Data collection. The study was carried out in the upper portion of the reservoir (10°42'29"S and 48°25'02"W), near Porto Nacional municipality (Tocantins State, Brazil). We sampled six sites distributed over approximately 15 km. We sampled shallow littoral areas of islands, bays and banks, covering habitats structured with logs, submerged trees and aquatic plants (especially *Najas microcarpa*, a submerged macrophyte).

Fish were sampled monthly between November 2010 and October 2011, except for December 2010 and January 2011, when sampling did not occur. Fish were caught with artificial lures (surface and subsurface action, 10-15 cm total length), rods and casting reels. Using a boat, baits were cast continuously in different habitats along the littoral zone, always during the day (08:00 - 18:00). At each site, fishing effort was standardized by number of fishermen and fishing time. Voucher specimens are deposited in the Coleção de Peixes do Laboratório de Ictiologia Sistemática, Universidade Federal do Tocantins, Porto Nacional, Brazil (UNT 12494).

All fish were immediately stored in ice and subsequently transferred to the laboratory at Núcleo de Estudos Ambientais (Neamb), Universidade Federal do Tocantins. We recorded from each specimen: total and standard length (TL and SL, cm), total weight (TW, g), gonad weight (GW, g), body weight (BW, body weight after evisceration, g), visceral fat (FW, g), stomach fullness (SF), sex and phase of gonad maturation. Stomach fullness was assessed by visual inspection and categorized as 0 (empty), 1 (1–25% of stomach volume occupied by food), 2 (26-75%) and 3 (76-100%). Stomachs with SF equal to 2 and 3 were preserved in formalin 4% for diet analysis; some stomachs with SF = 1 were also analyzed. Contents were identified under stereoscopic microscopy to the lowest taxonomic level; prey fish were identified following Lucinda *et al.* (2007). For each food item, volume (ml) was measured using graduated cylinders, and for each prey fish, standard length (cm) was measured with a ruler.

Phases of gonad maturation followed Brown-Peterson *et al.* (2011): Immature, Developing (which included Spawning Capable), Regressing and Regenerating. Gonad phases were assigned macroscopically considering characteristics of the gonads such as size, turgidity, irrigation, color and position in the abdominal cavity (Vazzoler, 1996). In the case of ovaries, the presence and size of oocytes were also considered.

Data analysis. Due to low fish abundance in some samples, we grouped months into six periods: Nov/2010; Feb-Mar/2011; Apr-May/2011; Jun-Jul/2011; Aug-Sep/2011; Oct/2011. For rarefaction analyzes (see below) we use a simplified grouping, in which months were combined into two seasons: wet (Nov/2010 to May/2011) and dry (Jun/2011 to Oct/2011).

We investigate temporal variation in feeding activity by calculating the frequency of SF values over periods, considering all fish captured. To investigate the diversity of food resources consumed and to compare sex, seasons (wet and dry) and maturity (immature and adult), we calculated resource accumulation curves based on sampling effort (number of stomachs). To build curves, sample order in the original matrix was randomized 50 times (EstiMateS 5.0 software; Colwell, 1997). For this analysis we considered only resources identified at some independent level, removing unidentified or combined items. To investigate variations in diet composition (volume matrix) with respect to sex, periods and maturity, a Non-Metric Multidimensional Scaling analysis (NMDS) was conducted based on Bray-Curtis distance (Past 1.75b software; Hammer *et al.*, 2001). Ontogenetic variations in diet were assessed by calculating the percent volume of resources consumed in different size classes (5 cm intervals SL). For the NMDS and ontogenetic analyses, we used a simplified resource matrix: fish prey were grouped into their respective taxonomic families (Engraulidae, Characidae, Curimatidae, Erythrinidae, Loricariidae, Cichlidae, Synbranchidae), and invertebrate prey were combined in "Invertebrate". Finally, to investigate the size of prey fish consumed by *C. piquiti*, we used Spearman's rank correlation to test the relationship between predator and prey standard lengths (SL).

To investigate reproductive dynamics, we calculated the percentage of gonad phases over periods. In addition, temporal variations in reproductive effort were evaluated with the gonad-somatic index: $GSI = (GW / TW) * 100$, considering only adult fish (separately for males and females). We also calculated the average size at first maturity, for sexes combined. Individuals were classified as adults and immature based on gonad inspection, and the frequency of adults in different classes of standard length (2 cm intervals) was calculated, following Vazzoler (1996). Length at first maturity was determined as L50 and L100, *i.e.* the average standard length within the class where at least 50% (L50) and 100% (L100) of individuals were adults.

To evaluate changes in energy allocation between somatic and reproductive activities, we examined variation in body condition, fat accumulation and reproductive effort (GSI). A covariance analysis (Ancova; Garcia-Berthou, 2001) was used to investigate variations in these traits among sexes, periods and the interaction sex*periods (categorical factors), conducted separately for immature and adults. For body condition, we considered body weight (BW) as dependent variable and standard length (SL) as covariate. For visceral fat (evaluated between April and October 2011), we considered fat weight (FW) as dependent variable and body weight (BW) as covariate. For reproductive effort, gonad weight (GW) was treated as dependent variable and body weight (BW) as covariate. All variables were log-transformed (Ln) and significant differences implied $p < 0.05$. Statistical tests were carried out in Statistica 7.1 (Statsoft, 2005).

Results

During the study period 270 specimens were captured (44% adults, 56% immature), being 109 females, 132 males and 29 undetermined. Total weight varied between 54.9 and 3352.8 g, while standard length ranged between 12.1 and 50 cm. Individuals were distributed in all size classes (5 cm intervals), however 82% showed LS < 30 cm.

Feeding ecology. There was a consistent high percentage of stomachs with food (SF > 1) over the periods; usually more than 50 % of stomachs had food (Table 1). Most immature fish showed stomachs with food (SF = 1 to 3) during all periods, while adults showed higher percentage between June and October (Table 1). We analyzed the content of 114 stomachs, distributed in all size classes. A total of 23 resources (70.3 % total volume) were identified at some independent level, including fish, insects, plants, crustaceans and mollusks. Other resources (29.3 % total volume) could not be identified beyond some broad level, and they were combined (within Class, Order, Family, Genus) or assigned as Unidentified (Table 2). Based on these 23 identified resources, the accumulation curve did not stabilize after 67 samples (Fig. 1), indicating that other resources will be recorded with new samples. This trend was observed for males and females, immature and adults, in dry and wet seasons (Fig. 1). For a same sampling effort, we recorded greater diversity of resources in the diet of immature fish, and during the wet season.

Table 1. Feeding activity of immature and adult *Cichla piquiti*, measured as the percentage of empty stomachs and stomachs with food (fullness categories combined, 1 to 3) over periods. N = number of stomachs analyzed.

Periods	Immature			Adults		
	N	Empty	With food	N	Empty	With food
Nov/10	24	41.7	58.3	8	37.5	62.5
Feb-Mar/2010	24	25.0	75.0	16	43.8	56.3
Apr-May/2010	15	20.0	80.0	26	53.8	46.2
Jun-Jul/2010	25	24.0	76.0	18	11.1	88.9
Aug-Sep/2010	25	32.0	68.0	24	29.2	70.8
Oct/2010	22	27.3	72.7	14	14.3	85.7

Table 2. Resources consumed by *Cichla piquiti* in Lajeado reservoir, rio Tocantins basin. The analysis is based on 114 stomachs. OC% = frequency of occurrence; VL% = relative volume; N = number of prey fish.

Resources	OC %	VL%	N
1. PLANTS			
ANGIOSPERMA			
"Macrophyte"	4.4	0.2	
2. INVERTEBRATES			
MOLLUSCA			
"Mollusk"	0.9	0.002	
ARTHROPODA			
Unidentified	0.9	0.002	
ODONATA			
"Larvae"	2.6	0.1	
CRUSTACEA			
DECAPODA			
"Shrimp"	1.8	0.1	
3. VERTEBRATES (FISH)			
Unidentified	58.8	20.9	
CLUPEIFORMES			
ENGRAULIDAE			
Anchoviella carrikeri (Fowler, 1940)	3.5	1.9	5
Unidentified	0.9	0.4	1
CHARACIFORMES			
Unidentified	0.9	0.005	1
CURIMATIDAE			
Cyphocharax festivus Vari, 1992	0.9	0.01	1
Unidentified	1.8	1.3	4
CHARACIDAE			
Hemigrammus sp. B	3.5	0.4	4
Hemigrammus sp. H	0.9	0.1	2
Hyphessobrycon spp.	0.9	0.1	1
Hyphessobrycon sp. B	0.9	0.2	1
Hyphessobrycon sp. D	0.9	0.01	1
Hyphessobrycon sp.	0.9	0.1	1
Metynnis spp.	8.8	5.7	10
Metynnis sp. 2	4.4	8.8	7
Metynnis sp. A	2.6	1.4	5
Myleus sp. A	1.8	13.1	2
Serrasalmus rhombeus (Linnaeus, 1766)	1.8	0.3	2
Serrapinnus spp.	0.9	0.1	1
Unidentified	3.5	0.2	4
ERYTHRINIDAE			
Hoplias malabaricus (Bloch, 1794)	1.8	5.0	2
SILURIFORMES			
LORICARIIDAE			
Loricariichthys sp.	0.9	6.1	1
SYNBRANCHIFORMES			
SYNBRANCHIDAE			
Synbranchus marmoratus (Bloch, 1795)	0.9	1.1	1
PECIFORMES			
CICHLIDAE			
Cichla piquiti Kullander & Ferreira, 2006	0.9	0.5	1
Cichla spp.	1.7	0.4	2
Cichlasoma araguaiense Kullander, 1983	9.6	16.0	12
Geophagus spp.	0.9	0.2	1
Geophagus sveni Lucinda, Lucena & Assis, 2010	0.9	2.4	1
Satanoperca jurupari (Heckel, 1840)	5.3	12.4	6
Unidentified	4.4	0.6	5

"Fish" was the main resource consumed, occurring in 92.7% of stomachs and summing 99.6% of total volume. At least 19 fish species were recorded in the diet, each with low occurrence, volume and abundance across stomachs (Table 2). The species more consumed belonged to the families Cichlidae and Characidae, particularly *Cichlasoma araguaiense*, *Satanoperca jurupari*, species of the genus *Metynnis* and small characins (*Hemigrammus* and *Hyphessobrycon*). The NMDS revealed no clear variation in diet between sexes, periods and maturity (Fig. 2). Considering size classes, there was no clear pattern of ontogenetic variation, with predominance of Characidae and Cichlidae in virtually all length classes (Table 3). The size of predators and prey were significantly correlated (Spearman: n = 76; R = 0.63; $p < 0.0001$), but *C. piquiti* consumed mainly fish smaller than 10 cm SL (Fig. 3). Prey larger than 6 cm SL were consumed only by predators larger than ~25 cm, while large prey were consumed occasionally. One exception was a predator with 21.7 cm that consumed a prey with 19 cm (*Synbranchus marmoratus*).

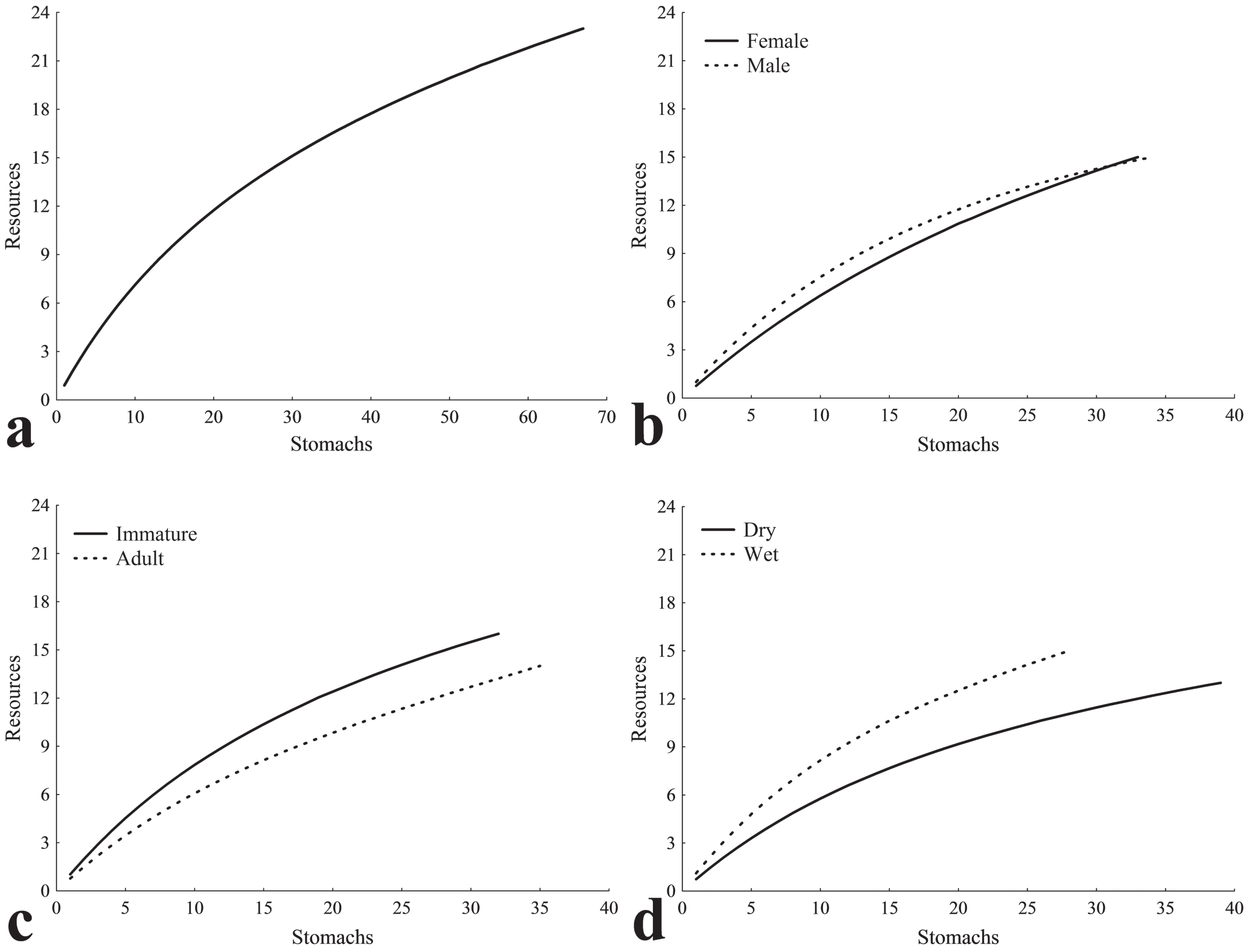

Fig. 1. Resource accumulation curves controlled by the number of stomachs of *Cichla piquiti* analyzed, considering all fish (a), sexes (b), maturity (c) and season (d). Sample size was reduced to 67 stomachs because this analysis considered only resources identified at some independent level, removing unidentified or combined items.

Table 3. Feeding resources (percent volume) consumed by different length classes (standard length SL, cm of *Cichla piquiti*). Resources are grouped in families or groups. Values above 10% are highlighted in gray. N = sample size. Mac. = macrophytes; Inv. = invertebrates; Eng. = Engraulidae; Cha. = Characidae; Cur. = Curimatidae; Ery. = Erythrinidae; Lor. = Loricariidae; Cic. = Cichlidae; Syn. = Synbranchidae.

Class	N	Mac.	Inv.	Eng.	Cha.	Cur.	Ery.	Lor.	Cic.	Syn.	Unidentified fish
10 - 14.9	3	0.00	0.00	0.00	47.62	0.00	0.00	0.00	0.00	0.00	52.38
15 - 19.9	31	0.06	0.05	5.22	21.78	0.00	0.00	0.00	33.83	0.00	39.06
20 - 24.9	69	0.72	0.64	7.88	26.58	5.69	0.00	0.00	27.35	4.73	26.43
25 - 29.9	32	0.00	0.15	0.00	32.39	0.00	16.72	0.00	36.38	0.00	14.35
30 - 34.9	15	0.08	0.00	0.00	40.46	0.00	0.00	0.00	25.77	0.00	33.69
35 - 39.9	6	0.30	0.00	0.00	0.00	0.00	0.00	0.00	61.26	0.00	38.44
40 - 44.9	7	0.00	0.22	0.00	67.37	0.00	9.98	0.00	21.32	0.00	1.11
45 - 49.9	1	0.00	0.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00	0.00

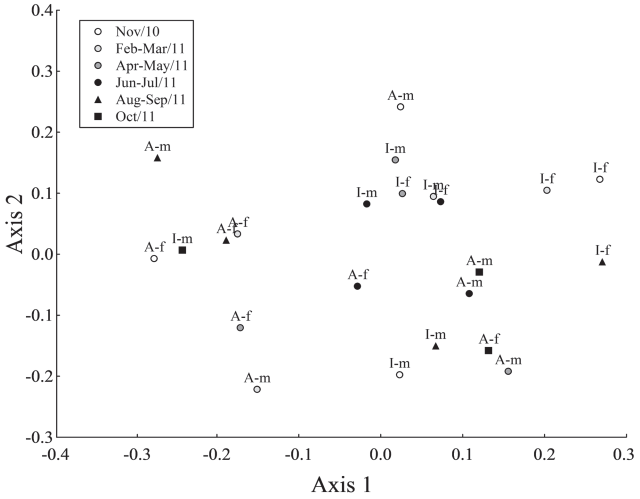

Fig. 2. Nonmetric multidimensional scaling (NMDS) applied to investigate variation in the diet of *Cichla piquiti* according to periods, sex (m = males; f = females) and maturity (I = immature; A = adult).

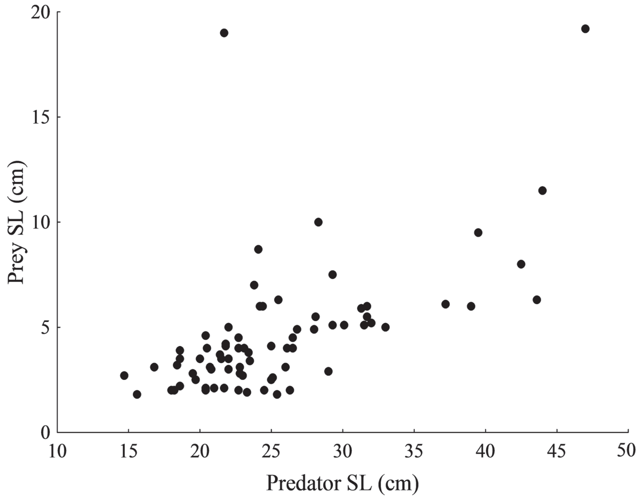

Fig. 3. Relationship between the size (standard length SL, cm) of *Cichla piquiti* and its prey.

Reproduction. We recorded all reproductive phases over the year (Fig. 4), indicating that the breeding season is long. Immature and reproductive individuals occurred in all periods, but fish with reproductive activity (*i.e.* Developing and Regressing) were more frequent between February and October (Fig. 4), especially in Apr-May/2011. Reproductive effort (GSI) also indicated a long breeding period, with effort concentrated between February and September (Fig. 5). However, mean gonad weight did not differ significantly among periods, but females showed heavier gonads than males (Ancova; Table 4). The high variability in reproductive effort within periods (Fig. 5), together with the coexistence of different gonad phases (Fig. 4), indicate that reproduction is not synchronized among individuals. The average standard length at first maturity (L50) was 24.6 cm (sexes pooled), and the average length in which all individuals are able to reproduce (L100) was 36.7 cm. The size of the smallest adult in the developing phase was 21.8 cm.

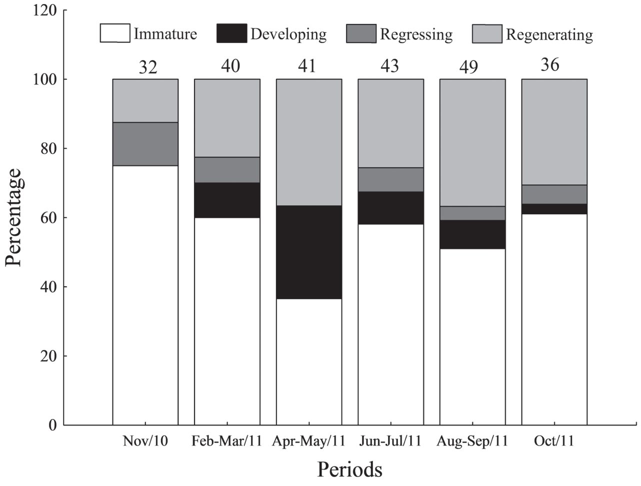

Fig. 4. Reproductive activity of *Cichla piquiti*, measured as the percentage of individuals in different reproductive phases within periods. Numbers above bars indicate sample size.

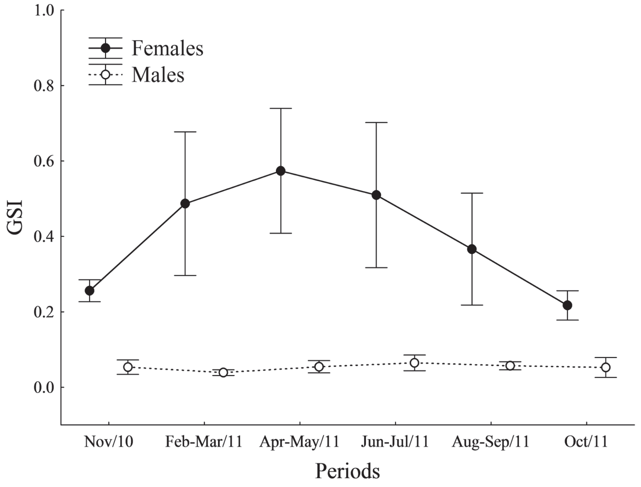

Fig. 5. Variation in reproductive effort of *Cichla piquiti* over time (mean ±SE), measured as the gonad-somatic index (GSI, %) calculated separately for males and females.

Energy allocation. For immature fish, covariance analysis showed no variation in body condition and fat accumulation among periods and sexes (Table 4), indicating the absence of temporal trade-offs in energy use (Fig. 6a, c). For adults, covariance analysis showed no variation in body condition (Fig. 6b), but fat accumulation varied significantly among periods and sexes (Table 4). In the case, adult fish accumulate more fat in the late dry and early rainy seasons (October), and females accumulated more fat than males (Fig. 6d).

Table 4. Analysis of covariance (Ancova) testing variations in body condition (body weight, g), fat accumulation (g) and reproductive effort (GSI) among sexes, periods and the interaction sex*period (categorical factors).

Factors	Adults			Immature		
	DF	F	P	DF	F	P
BODY CONDITION						
Intercept	1	511.0	0.0000	1	267.1	0.0000
Standard lenght (covariable)	1	3429.0	0.0000	1	1977.3	0.0000
Sex	1	0.3	0.5896	1	0.7	0.4213
Period	5	1.2	0.3320	5	0.3	0.9032
Sex*Period	5	0.8	0.5784	5	1.4	0.2371
Error	91			121		
FAT ACCUMULATION						
Intercept	1	21.6	0.0000	1	10.5	0.0019
Body Weight (covariable)	1	28.9	0.0000	1	12.8	0.0006
Sex	1	7.0	0.0099	1	1.2	0.2714
Period	3	3.6	0.0182	3	1.0	0.3764
Sex*Period	3	1.1	0.3362	3	0.6	0.6116
Error	71			68		
REPRODUCTIVE EFFORT (GSI)						
Intercept	1	56.4	0.0000			
Body Weight (covariable)	1	75.1	0.0000			
Sex	1	64.0	0.0000			
Period	5	1.7	0.1515			
Sex*Period	5	1.1	0.3713			
Error	91					

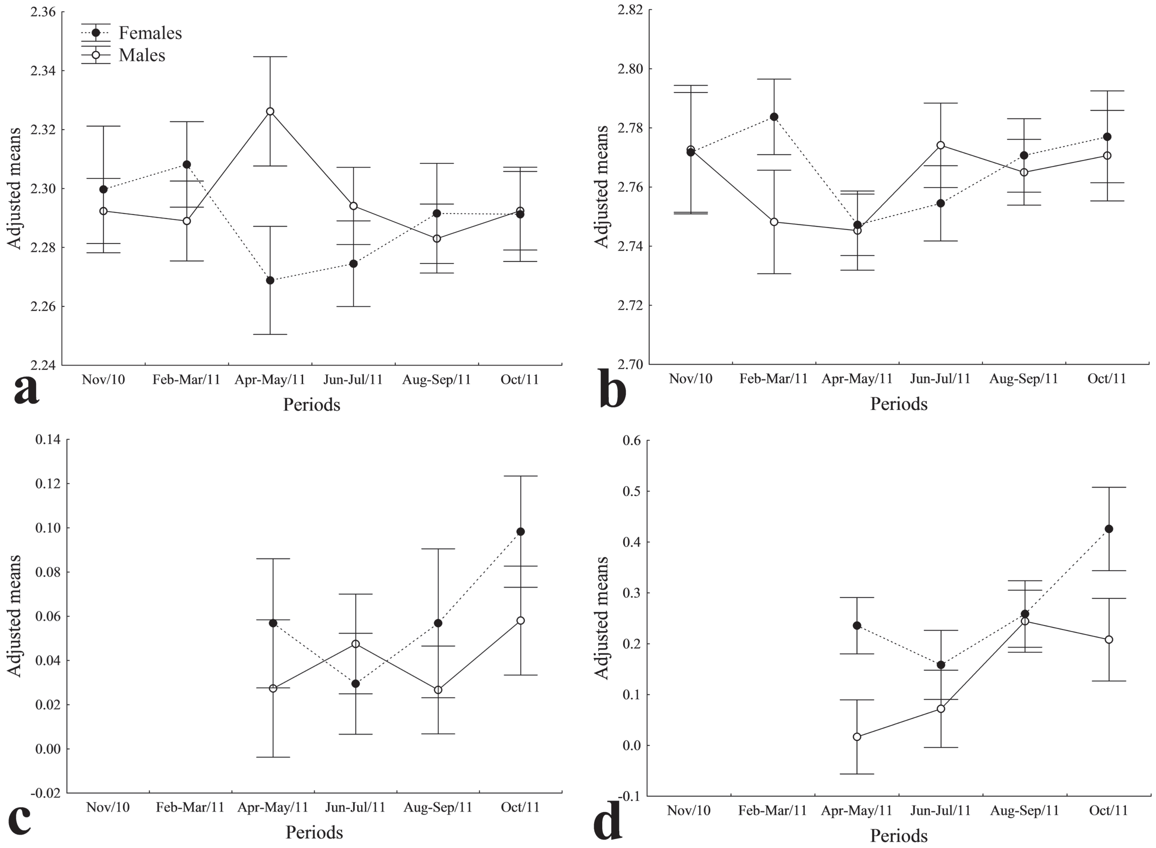

Fig. 6. Temporal variation in body condition and fat storage for immature (a and c respectively) and adult fish (b and d respectively of *Cichla piquiti*). These figures show adjusted means ±SE derived from an Analysis of Covariance (see Table 4).

Discussion

This study provided information on the ecology of *Cichla piquiti* within its natural range, *i.e.* Lajeado reservoir, rio Tocantins. The species is essentially piscivorous and consumes a diversity of small-sized fishes in the reservoir. The reproductive period is long, considering that reproductive individuals and immature fish were recorded in all periods. In addition, the absence of temporal variation in body condition and gonad weight indicates the absence of temporal trade-offs in energy allocation. *Cichla piquiti* probably found adequate conditions in the reservoir to feed and reproduce all over the year.

Although Neotropical fishes are characterized by high feeding plasticity (Abelha *et al*., 2001), some species exhibit food preferences or even trophic specialization. *Cichla piquiti* had restrict piscivorous behavior (a common pattern in *Cichla*; Jepsen *et al*., 1997; Novaes *et al*., 2004; Montaña *et al*., 2011), with little influence of season, sex and ontogeny. It is likely that small predators (< 10 cm SL) consume other resources, such as invertebrates (*e.g*., Rabelo & Araújo-Lima, 2002), but these small fish were absent from samples (as were large individuals); our inferences are valid to *C. piquiti* between 15 and 45 cm SL. For this size range, small-sized Characidae and Cichlidae fish were the most consumed prey, probably because these groups dominate fish assemblages in South American reservoirs (Agostinho *et al*., 2007), and co-occur with *Cichla* in shallow littoral areas. In addition, these predators usually prefer small prey, with approximately one third of its size (Jepsen *et al*., 1997; Winemiller *et al*., 1997); in fact, most prey consumed were < 10 cm standard length. It is likely, therefore, that the strict piscivorous behavior of *C. piquiti* is associated with a high diversity and abundance of small-sized fish in littoral areas of the reservoir, as small-sized species are common in the rio Tocantins basin (Lucinda *et al*., 2007; Soares *et al*., 2009). In addition, the high occurrence of stomachs with food contrasts with patterns found for piscivorous fish, in which empty stomachs prevail (Jepsen *et al*., 1997; Arrington *et al*., 2002; Bacheler *et al*., 2004), indicating resource availability and continuous feeding activity in Lajeado reservoir.

Cichla piquiti was essentially piscivore, but its diet was diverse and included 23 resources. Moreover, unidentified fish summed a significant portion of consumed resources and accumulation curves did not stabilize after 67 samples, indicating that other resources would be recorded with additional sampling effort. A diverse diet has been reported in other Amazonian systems, with predominance of fish and low rates of cannibalism (Jepsen *et al.,* 1997; Winemiller, 2001; Montaña *et al.,* 2011). When *Cichla* is non-native, however, its diet is poor and based on cannibalism, invertebrates and a few non-native fish (Fugi *et al.,* 2008; Capra & Benneman, 2009; Villares Junior & Gomiero, 2010; Santos *et al.,* 2011). In Lajeado reservoir, cannibalism and non-fish resources summed less than 1% of all volume ingested. These trends and comparisons may shed light on understanding the disturbance caused by *Cichla* when introduced into non-Amazonian reservoirs. While severe impacts have been reported elsewhere (Pinto-Coelho *et al.,* 2008; Pelicice & Agostinho, 2009; Menezes *et al.,* 2012), there is no evidence of disturbance in Amazonian reservoirs. There are some competing/complementary hypothesis to explain its nuisance behavior when non-native (*e.g*., voracity, naiveté effect, lack of refuges, pulse of young predators; see Pelicice *et al*., 2015), but the high diversity of prey resources in Amazonian ecosystems may play a role in mitigating strong predatory effects. These systems are characterized by a mega-diversity of small-sized fish (Lowe-McConnell, 1999; Santos & Ferreira, 1999), which may represent a variety of resource options and avoid the excessive pressure upon a small set of populations. In fact, *C. piquiti* consumed at least 19 fish species, each with low occurrence, volume and number (Table 2), indicating that each prey species is consumed sporadically. In non-Amazonian reservoirs, especially in the Paraná, where *Cichla* has been intensely introduced, the diversity of small fish is remarkably lower (Pelicice *et al*., 2005; Agostinho *et al*., 2007), a scenario in which resource options are more limited and the recovery of populations in demographic decline is difficult. Thus, we believe that, in Amazonian reservoirs, *Cichla* is maintained by the alternate use of different prey populations, a mechanism (portfolio effect; Tilman, 1999) that must prevent strong demographic effects, over-exploitation and extirpation. Future studies should devote more attention to the role played by resource diversity/shortage as a mechanism mediating ecosystem effects caused by *Cichla*.

As expected, *C. piquiti* showed a long reproductive period in Lajeado reservoir. Reproductive and immature fish were recorded in all sampling months and gonad weight (GSI) did not differ among periods. In addition, the high variability in reproductive effort within periods, together with the coexistence of different gonad phases, suggest asynchrony in gonad development among individuals. Therefore, reproduction is probably occurring all over the year, *i.e.* part of the population is always committed with reproduction in some period. Impoundments stabilize the water level and create extensive littoral areas with shallow and highly structured habitats, conditions that provide opportunity for reproduction. *Cichla* species usually demand hydrological stability (*i.e.* low water level variation) and shallow areas to build nests and protect their fry (Winemiller, 2001; Muñoz *et al*., 2006), so Lajeado reservoir must offer adequate breeding conditions for *C. piquiti*. In addition, the regional climate in the Tocantins basin is tropical warm, so temperature is not a limiting factor. In southern basins, where seasonal variation in temperature is remarkable (warm summers and cold winters), reproduction is restricted to warm months (Souza *et al.,* 2008; Gomiero *et al.,* 2009; Vieira *et al.,* 2009; Pelicice *et al*., 2015). Therefore, environmental stability in Lajeado (water level and temperature) may explain the absence of trade-offs in energy allocation over the year, since reproductive and feeding activities are continuous among different individuals of the population.

Although covariance analysis showed no statistical difference in gonad weight among periods, higher values of reproductive effort (GSI) were observed during the beginning of the dry season, with a high percentage of reproductive fish in April and May. In addition, adult fish accumulated fat tissue in the late dry season, coinciding with higher feeding activity. This pattern may be associated with environmental triggers (*e.g.*, photoperiod, small variations in temperature and water transparency), or even residual behavior (endogenous factors) related to reproduction in natural conditions, *i.e. Cichla* usually reproduces during low water periods under a natural fluvial regime (Jepsen *et al.*, 1999; Muñoz *et al.*, 2006). In Venezuela, Jepsen *et al.* (1997, 1999) found trade offs between body condition and reproduction, demonstrating that *Cichla* species experience clear temporal variation in energy use via synchronized development of gonads, spawning, parental care (building and protection of nests) and growing. Considering that *C. piquiti* accumulated reserves in the late dry season while body condition and reproductive effort showed no significant variation, future studies must investigate changes in the reproductive behavior. The breeding period, for example, might be expanding, as Lajeado reservoir was young (10 years old) when this study was carried out. Future studies must also monitor *C. piquiti* populations on a monthly basis during a whole year (*i.e.* the present study did not sample December and January), and histological analysis should confirm gonad phases on a finer level. Behavioral aspects of reproduction (mating, nest construction, defense) must also be addressed, considering that females accumulated more fat tissue than males. Females may show greater demand for reserves, probably used in the production of gametes (gonads of females were heavier than males) and in the protection of nests and fry.

Cichla species have obtained ecological and economic relevance in Amazonian impoundments (Santos & Oliveira Junior, 1999; Camargo & Petrere Jr., 2004) and in reservoirs located elsewhere (Agostinho *et al.*, 2007). This trend is also occurring in Lajeado reservoir, where *C. piquiti* has been increasingly targeted by commercial and sport fisheries. Fishing effort has increased and focused especially on *C. piquiti*, mainly because large migratory species have declined, and recreational, sport and commercial fishing, together with tournaments, have experienced significant development during past years. Increasing fishing effort on a single stock, however, can severely disrupt population structure, leading to demographic effects and overfishing (Allan *et al.*, 2005). The lack of inspection in Lajeado reservoir, for example, has led to the use of predatory fishing methods (*e.g.*, harpoons), which targeted large individuals and may have removed mega-spawners from the population (Froese, 2004). It must cause concern because extensive removal of top predators may affect food web structure and ecosystem functioning (Britten *et al.*, 2014), with negative consequences for recruitment and fisheries. Management measures must, therefore, devote attention to *C. piquiti* as a means to maintain persistent stocks and ecosystem services (*i.e.* fishery) in the reservoir. At present, fishing closures to protect reproduction (*i.e.* defeso, November to February) are the main management action in the region, but other measures must be considered to provide protection to juveniles (minimum capture size) and adults (incentive to catch and release, establishment of quotas, banning of predatory fishing methods). We hope that agencies responsible for regulation, promotion and enforcement of fishing activities in the rio Tocantins (*e.g.*, Instituto Natureza do Tocantins, Naturatins; Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis, IBAMA; Ministério da Pesca e Aquicultura, MPA) use the information presented here to improve management practices. In this respect, local fishermen and riverine communities could play a positive role (*e.g.*, inspection, promoting catch and release), especially if they were educated with sound technical information.

In conclusion, *C. piquiti* established populations in Lajeado reservoir; it seemed adapted to use resources of the impoundment, with recruitment occurring over the year. Biological traits like parental care and prolonged reproductive activity, together with prey availability, may have played a role facilitating the colonization and establishment of populations. We hope that these results indicate efficient management measures to protect *C. piquiti* under a scenario of increasing fishing pressure. Furthermore, we expect that our study, which investigated *C. piquiti* within its native range, throw some light about the disturbance caused by *Cichla* in non-Amazonian reservoirs. Understanding differences in feeding and reproductive dynamics between native and non-native populations, for example, can stimulate the formulation of hypotheses to explain why *Cichla* is so harmful when introduced - an issue still unresolved.

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