Neotropical Ichthyology, 12(3): 649-658, 2014

DOI: 10.1590/1982-0224-20130186

Short-term changes in energy allocation by Hemiodontidae fish after the construction of a large reservoir (Lajeado Dam, Tocantins River)

Estevão Rodrigues Medeiros[1], Fernando Mayer Pelicice[2], Carlos Sergio Agostinho[2], and Elineide Eugênio Marques[2]

The present study investigated energy allocation patterns in three fish species from the family Hemiodontidae (*Argonectes robertsi*, *Hemiodus microlepis*, and *Hemiodus unimaculatus*), before and after the construction of Lajeado Dam, Tocantins River, Amazon basin. Changes in the use of energy (between somatic and reproductive processes) were indirectly evaluated by means of temporal variations in fish body condition, feeding activity, visceral fat storage, and reproductive effort. Fish were collected from October 1999 to September 2004, in periods that preceded and followed the construction of the dam. We recorded significant changes in all ecological traits for the three analyzed species (for males and females). In general, there was an intense reduction in reproductive activity after river damming, whereas visceral fat and body condition increased consistently. In contrast, there was no clear trend in feeding activity (*i.e.*, stomach weight), with little changes in species diet during the analyzed period. These results indicate that the impoundment changed the energy allocation process between somatic and reproductive activities, since fish started to allocate energy mainly to somatic processes. These changes may have a negative effect on the persistence of populations in Lajeado Reservoir, because improvements in somatic condition will not necessarily translate into increased fitness.

Neste estudo buscou-se avaliar padrões na alocação de energia em três espécies de peixes da família Hemiodontidae (*Argonectes robertsi*, *Hemiodus microlepis* e *Hemiodus unimaculatus*), antes e após a construção da UHE Lajeado, rio Tocantins, bacia Amazônica. Alterações no uso da energia (entre atividades somáticas e reprodutivas) foram avaliadas de maneira indireta, através de variações temporais na condição corporal dos peixes, atividade alimentar, acúmulo de gordura visceral e esforço reprodutivo. Os peixes foram coletados no trecho afetado pela barragem entre outubro de 1999 e setembro de 2004, envolvendo períodos que antecederam e sucederam a formação do reservatório. Registramos alterações significativas nos valores dos atributos medidos, para peixes machos e fêmeas das três espécies analisadas. De maneira geral, houve intensa redução na atividade reprodutiva nos anos que seguiram ao barramento, enquanto que registramos acúmulo de gordura visceral e aumento na massa corporal das espécies. Por outro lado, não houve um padrão claro de variação na atividade alimentar (*i.e.*, peso dos estômagos), assim como registramos pouca alteração na dieta das espécies entre os períodos. Esses resultados indicam que o represamento alterou o processo de alocação de energia entre atividades somáticas e de reprodução, já que os peixes passaram a direcionar a energia adquirida via alimentação principalmente para processos somáticos. Podemos prever, com isso, que as alterações observadas tenham efeitos negativos na persistência das populações em Lajeado, já que o aumento na condição individual não deve acarretar necessariamente em aumentos no fitness dos peixes.

Key words: Body condition, Colonization, Fitness, Reproduction, River regulation.

Introduction

Large impoundments, especially those for hydropower generation, are found in all Brazilian basins. Although they provide undeniable social and economic benefits, they also cause significant negative effects on the fish fauna (Agostinho *et al.*, 2007). Many studies have documented changes in species abundance and composition in areas affected by large dams, resulting in significant alterations in the structure of populations and assemblages (*e.g.*, Santos, 1995; Mérona *et al.*, 2001; Agostinho *et al.*, 2008; Petesse & Petrere Jr., 2012; Araújo *et al.*, 2013). Most Neotropical fish species do not colonize the reservoir environment because of ecological restrictions imposed by the loss of resources, habitats and conditions, which are important to specific life history stages such as growth, maintenance and reproduction (Agostinho *et al.*, 2007). The persistence of

---

[1] Programa de Pós-Graduação em Ecologia de Ecótonos, Universidade Federal do Tocantins, Porto Nacional, Tocantins. medeiros.er@gmail.com
[2] Núcleo de Estudos Ambientais (Neamb), Universidade Federal do Tocantins. Jardim dos Ipês, 77500-000 Porto Nacional, TO, Brazil. fmpelicice@gmail.com, agostinhocs@gmail.com, emarques@mail.uft.edu.br

populations, in areas affected by large impoundments, will depend on the ability of some species to acquire and use the energy resources available in the new environment.

Fish, like other animals, use the energy acquired through feeding in somatic processes (growth, maintenance, and storage) and/or gamete production (Vazzoler, 1996; Heino & Kaitala, 1999; McBride *et al.*, in press). Depending on life-history strategies or life cycle phases, fish can prioritize a particular process (*i.e.*, growth, when immature) or allocate energy to different processes (*i.e.*, maintenance and reproduction, when adults). As many South American species present seasonal reproductive dynamics, it is common to observe temporal variations in the use of energy, including periods of accumulation (*i.e.*, tissue formation) followed by periods of gamete production (Bailly *et al.*, 2008; Santos *et al.*, 2010; Peressin *et al.*, 2012). Changes in such use are expected when rivers are dammed (Abujanra *et al.*, 2009), since reservoirs change the availability of food resources (Mérona *et al.*, 2003; Loureiro-Crippa & Hahn, 2006; Luz-Agostinho *et al.*, 2006) and environmental triggers and conditions (*e.g.*, duration and timing of floods, water flow, conductivity, and transparency) that stimulate and allow reproductive dynamics (Agostinho *et al.*, 2004). We can predict, for example, that decreases in feeding activity (*i.e.*, absence of preferential resources) will cause decreases in growth and reproductive activity; on the other hand, the suppression of reproduction (*i.e.*, the absence of environmental triggers) will result in intense somatic growth or energy storage, but with decreased fitness of individuals. Understanding changes in the use of energy, therefore, may help explaining the colonization process in reservoirs, since variations in the acquisition and use of energy determine the success of species in occupying the new environment.

Variations in energy use between somatic and reproductive processes can be indirectly assessed by means of simple metrics, such as fish body condition, feeding activity, visceral fat accumulation and reproductive effort (*e.g.*, Ballón *et al.*, 2008; Walsh *et al.*, 2012). In this case, variation in these traits, together with their relationship, can be used to evaluate changes in the use of energy. Following this perspective, the present study investigated changes in energy allocation in three species of the family Hemiodontidae, before and after the construction of Lajeado Dam, Tocantins River. Species from this family, which present a rheophilic and/or migratory behavior (Neuberger *et al.*, 2009), are frequently captured in rivers and reservoirs of the Amazon basin (Santos, 1995; Santos *et al.*, 2004; Soares *et al.*, 2009), allowing analyses with an extensive data set. The current study investigated temporal changes in body condition, feeding patterns, visceral fat and reproductive effort for *Argonectes robertsi* Langeani, 1999, *Hemiodus microlepis* Kner, 1858, and *Hemiodus unimaculatus* (Bloch, 1794), in periods that preceded and followed the impoundment.

Material and Methods

Study Area

The Tocantins River, together with the Araguaia River, 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 River. The pluvial regime is seasonal (wet season between October and April), with a marked period of high waters (*ca.*, 10 m amplitude; Mérona *et al*., 2010). At present, however, 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 under the influence of Lajeado Dam (Luis Eduardo Magalhães Hydroelectric Plant; 902.5 MW installed capacity), located in the middle/upper portion of the basin (09º47'S 48º2'W). Closed in October 2001, the dam formed a large 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 December 2013).

Previous monitoring carried out in the area (Lucinda *et al*., 2007) recorded six species of the family Hemiodontidae: *Argonectes robertsi* Langeani, 1999, *Hemiodus microlepis* Kner, 1858, *Hemiodus unimaculatus* (Bloch, 1794), *Hemiodus ternetzi* Myers, 1927, *Bivibranchia velox* (Eigenmann & Myers, 1927), and *Bivibranchia fowleri* (Steindachner, 1908). The species *H. ternetzi*, *B. velox*, and *B. fowleri* have been rarely captured, whereas *A. robertsi*, *H. microlepis*, and *H. unimaculatus* were among the 15 most abundant species in the area (ERM, pers. obs.). Therefore, the present study investigated only the three last species that, together, constituted a considerable sample size (n = 13,187 individuals, collected over a four years period). According to Neuberger *et al.* (2009), only *A. robertsi* is a long distance migratory species, while the others are sedentary or short distance migratory.

Data sampling

Data sampling was carried out in 13 sites distributed along the Tocantins River and its main tributaries, covering all the extension affected by the impoundment (*ca.*, 150 km). Five sites were located in the upper fluvial region (fluvial zone), four in the middle region (transition zone) and four in the lentic area closer to the dam (lacustrine zone). Sampling occurred on a monthly basis, from October 1999 to September 2004, including periods that preceded and followed the construction of the dam.

Fish were collected with gillnets (14 mesh sizes, 2.4 to 18cm between opposite knots), exposed for 24 hours in each

Table 1. Results of linear regressions between standard length (SL, cm) and stomach weight (SW, g) and total weight (TW, g, discounting gonad weight), conducted separately by species and sex. Standard residuals from each regression were used as a measure of feeding activity (SL x SW) and body condition (SL x TW).

	SL x SW (feeding)				SL x TW (condition)			
	r	df	F	p	r	df	F	p
A. robertsi								
Female	0.71	1.1402	1436.4	0.000001	0.98	1.1434	35959.9	0.000001
Male	0.75	1.974	1245.9	0.000001	0.99	1.1003	44448.2	0.000001
H. microlepis								
Female	0.82	1.2328	4713.5	0.000001	0.99	1.2646	89220.6	0.000001
Male	0.77	1.2527	3557.6	0.000001	0.99	1.2968	100413	0.000001
H. unimaculatus								
Female	0.67	1.2657	2151.8	0.000001	0.98	1.2905	85277.5	0.000001
Male	0.65	1.1856	1345.2	0.000001	0.98	1.2219	60244.8	0.000001

site (checked at 08h00 am, 04h00 pm and 10h00 pm). All individuals were identified, measured (standard length, SL, cm), weighted (TW, g) and gutted; the stomachs were preserved in formalin 4% for further analysis. We also recorded stomach (SW, g) and gonad (GW, g) weight of each individual, and determined gender through gonad inspection. The storage of visceral fat in the abdominal cavity was evaluated by means of a standardized scale of integer values, varying from zero (minimum) to three (maximum). In the case: 0 = absence, 1 = minimal presence of fat; 2 = organs partially covered with fat; 3 = organs completely covered with fat.

Voucher specimens are deposited in the Coleção de Peixes do Laboratório de Ictiologia Sistemática, Universidade Federal do Tocantins, Porto Nacional, Brazil (*A. robertsi*: UNT 1364; *H. microlepis*: UNT 1314; *H. unimaculatus*: UNT 1303).

Data Analysis

To analyze variations in energy allocation over the years, samples were combined into four different periods. Two represent the two years before the impoundment: (i) Pre-1 (October/99 to September/00) and (ii) Pre-2 (October/00 to

Table 2. Total fish captured (N) and length structure (standard length, cm) of *H. unimaculatus*, *H. microlepis* and *A. robertsi* before (Pre) and after (Post) the formation of Lajeado Reservoir. SD = standard deviation.

	Female					Male				
		Standard Length					Standard Length			
	N	mean	SD	min.	max.	N	mean	SD	min.	max.
A. robertsi										
Pre-1	592	14.9	3.8	7.5	25.0	572	12.4	3.2	6.6	20.0
Pre-2	463	13.7	3.3	7.0	23.7	331	12.1	2.7	7.5	20.3
Post-1	1012	16.4	3.5	7.4	22.6	331	14.5	2.3	9.0	24.0
Post-2	840	16.7	3.2	8.0	24.5	987	12.2	3.6	6.8	21.2
H. microlepis										
Pre-1	362	14.1	4.0	7.4	23.7	301	11.6	3.1	7.4	26.0
Pre-2	262	16.3	3.0	7.9	23.0	154	13.5	2.6	7.5	18.0
Post-1	1291	18.1	4.3	6.4	23.6	1706	16.4	4.0	5.2	23.0
Post-2	733	13.7	4.0	8.0	23.0	809	13.5	4.4	8.0	26.8
H. unimaculatus										
Pre-1	53	25.4	4.3	15.0	33.5	72	22.3	4.2	11.5	31.0
Pre-2	55	27.0	4.1	13.2	33.0	44	21.9	3.5	11.3	27.5
Post-1	710	18.4	3.5	8.2	30.5	688	16.5	3.9	8.4	28.2
Post-2	618	21.7	2.5	10.0	28.0	201	20.1	3.4	10.2	27.0

September/01). The other two represent, respectively, the second and the third year after the impoundment: (iii) Post-1 (October/02 to September/03) and Post-2 (October/03 to September/04).

Four ecological traits were used to assess the variation in energy allocation over the periods: feeding activity, body condition, visceral fat storage, and reproductive effort. Feeding activity is understood here as the amount of food in the stomach, measured as the stomach weight (SW) controlled by fish length (SL). For this variable, we used the standard residuals generated by the linear regression between SL x SW, conducted separately by species and sex (Table 1). Body condition, an indication of physiological state, was measured as fish weight (TW) controlled by length (SL) (Hoeinghaus *et al.*, 2006). For this variable, we used the standard residuals generated by the linear regression between SL x TW, conducted separately by species and sex (Table 1). To restrict this analysis to somatic condition, gonad weight (GW) was discounted from TW, and the resulting value was used in regressions. All variables used in regression analyses were log-transformed (Ln). Visceral fat in the abdominal cavity was evaluated following the established scale (0 to 3). Finally, reproductive effort was defined as the ratio between gonad weight and total body weight (GW/TW), again calculated separately by species and sex.

To examine changes in energy allocation among periods (Pre-1 and Pre-2, Post-1 and 2), statistical differences in feeding activity, body condition, fat storage and reproductive effort were tested by non-parametric Analysis of Variance (Kruskal-Wallis), conducted separately by species and sex. We also investigated the correlation (Spearman rank) among all attributes. We chose non-parametric analyses due to problems with heteroscedasticity among groups. Statistical significance, for all tests, implied $\alpha < 0.05$. Statistical analyses were performed in Statistica v. 7.1 (StatSoft, 2005). Because changes in length structure between Pre and Post-impoundment periods may influence the allocation of energy (*i.e.*, predominance of immature or adult), we calculated mean standard length (standard deviation, minimum and maximum) in each period, separately by species and sex.

Because changes in diet may replace energy sources and change assimilation (Benedito-Cecílio *et al.*, 2004; Davis *et al.*, 2012), we investigated variations in the use of feeding resources among periods. Stomach contents of seventy two adult fish were examined under a stereoscopic microscope, and resources were identified to the smallest possible taxonomic level. Stomachs were randomly chosen and included fish sampled in different sites along the river, totaling 12 stomachs for each species in each period (Pre and Post). The recorded feeding resources were grouped in seven categories: Algae (Filamentous: Chlorophyceae, Cyanophyceae, Ulotrichophyceae; non-filamentous: Bacillariophyceae, Euclorophyceae, Zygnemaphyceae); Detritus/Sediment (organic matter and inorganic particulate, with unknown origin); Aquatic Insects (Ephemeroptera, Odonata, Trichoptera, Ceratopogonidae, Chaoboridae, and

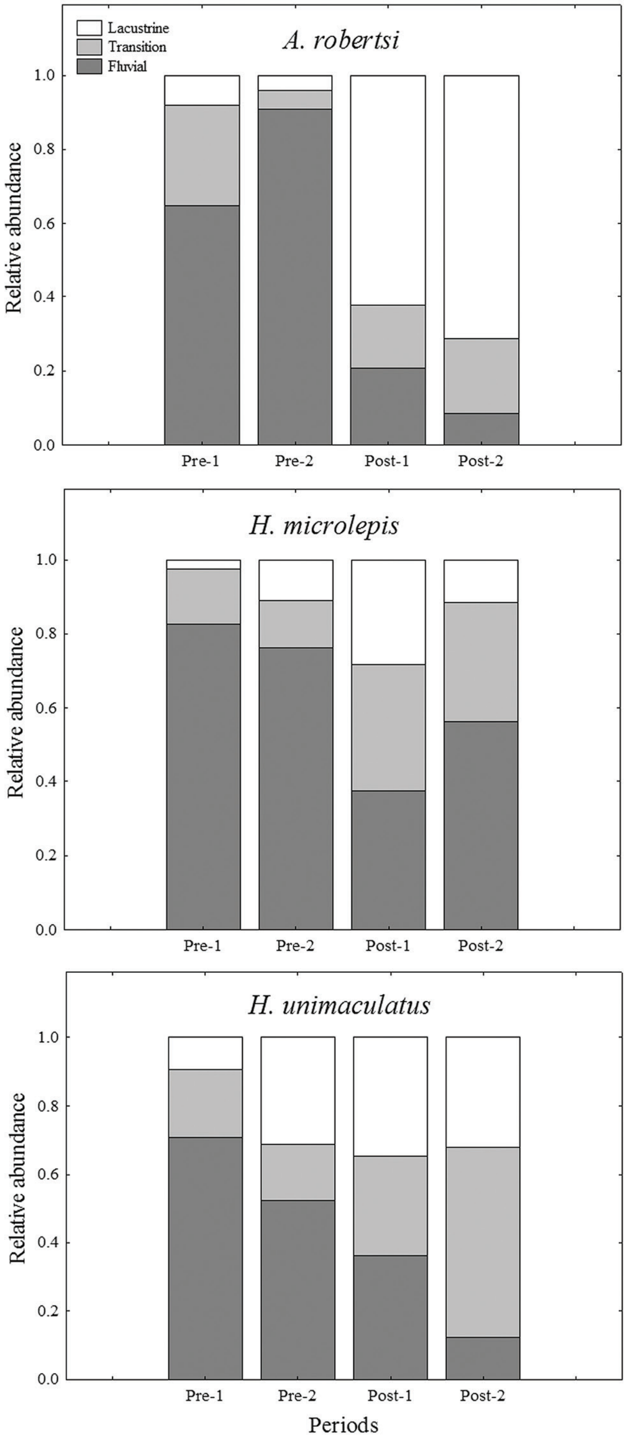

Fig. 1. Relative abundance of *A. robertsi*, *H. microlepis*, and *H. unimaculatus* in Pre- and Post-impoundment periods, in sites distributed along the reservoir (combined within zones: Fluvial, Transition, and Lacustrine).

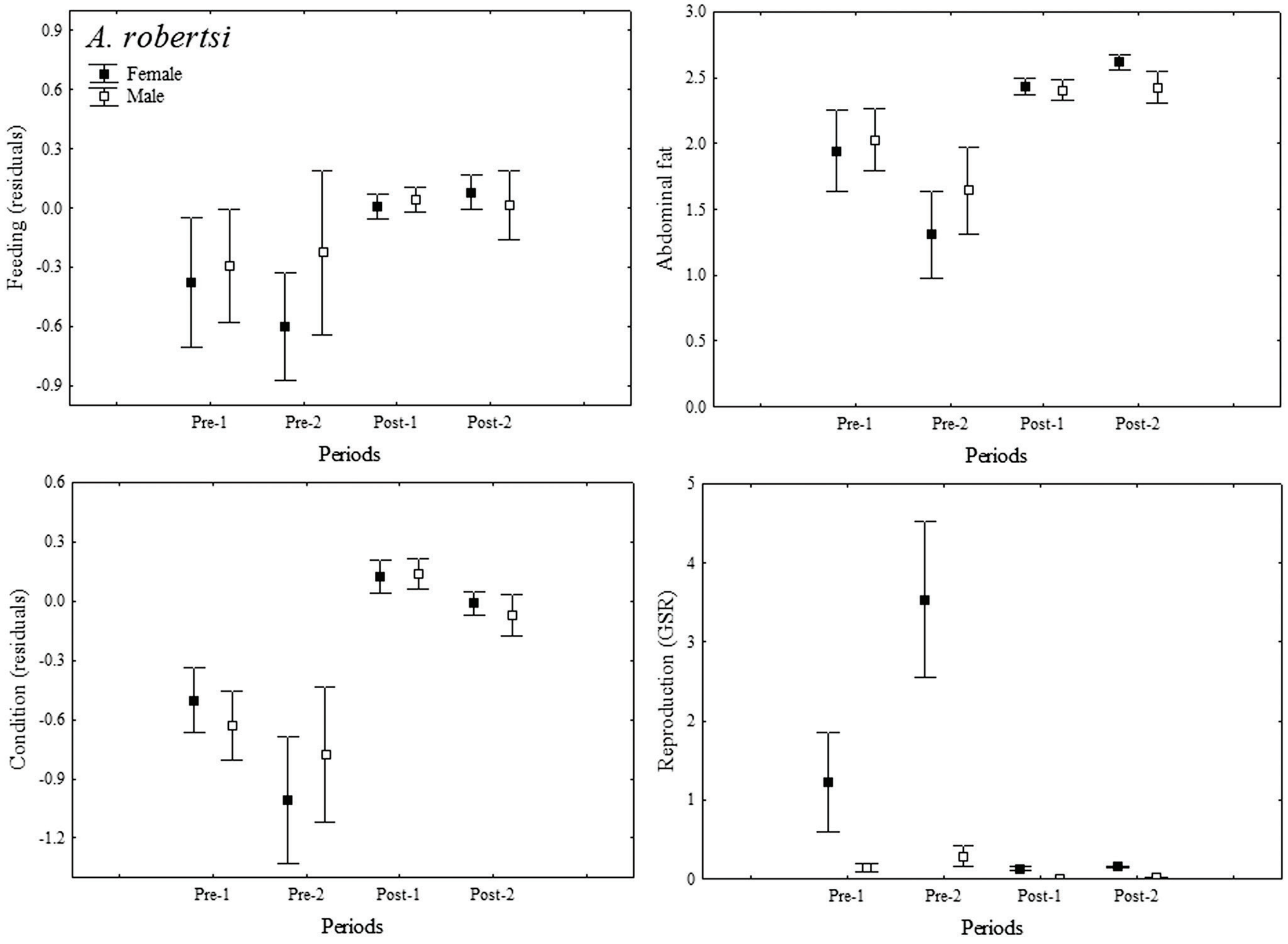

Fig. 2. Variation in feeding activity (standard residuals, regression between LS x WS), visceral fat storage, body condition (standard residuals, regression between LS x TW) and reproductive effort (GSR) of *Argonectes robertsi*, before (Pre-1 and 2) and after (Post-1 and 2) the construction of Lajeado Dam.

Chironomidae); Terrestrial Insects (Coleoptera, Hemiptera, and Hymenoptera); Other invertebrates (Acari, Bivalves, Crustaceans, spores of Porifera, Gastropods, Hydrachnidia, Nematoda, Oligochaeta, and Rotifers); Micro-crustaceans (Cladocerans, Ostracoda) and Vegetal (Bryophyte, spores, and seeds). Species diet, before and after the impoundment, was characterized as occurrence and volume (percentage) of each resource category. Diet similarity (volume) among periods was measured with Pianka's overlap index, using the software Ecosim v.7.2 (Gotelli & Entsminger, 2001).

Results

A total of 13,187 individuals were captured and analyzed (Table 2), being 2,441 *A. robertsi* (Pre = 9.2%; Post = 90.8%), 5,618 *H. microlepis* (Pre = 19.2%; Post = 80.8%) and 5,128 *H. unimaculatus* (Pre = 38.2%; Post = 61.8%). Variation in length structure showed no clear trend among periods, for both males and females (Table 2).

Argonectes robertsi

In Pre-impoundment periods, *A. robertsi* was captured mainly in upper sites; after the impoundment, most individuals were captured in the Lacustrine zone of the reservoir (Fig. 1). There were significant changes, for both sexes, in feeding activity (Kruskall-Wallis, $H_{female} = 34.3$; $p < 0.00001$; $H_{male} = 25.3$; $p = 0.00001$), fat storage ($H_{female} = 98.5$; $p < 0.0001$; $H_{male} = 38.7$; $p < 0.00001$), body condition ($H_{female} = 98.9$; $p < 0.0001$; $H_{male} = 85.1$; $p < 0.00001$) and reproductive effort ($H_{female} = 277.4$; $p < 0.0001$; $H_{male} = 265.4$; $p < 0.0001$) between Pre and Post-impoundment periods. In this case, higher feeding activity, fat storage and body condition were recorded in post-impoundment periods (Fig. 2). Reproductive effort, on the other hand, showed a significant reduction after the impoundment, especially for females (Fig. 2). We also recorded, in Post periods, considerable reduction in data variability (IC 95%). For females, reproductive effort correlated negatively

Table 3. Correlation (Spearman rank) among ecological traits measured in populations of *A. robertsi*, *H. microlepis*, and *H. unimaculatus*. Females = upper diagonal; Males: lower diagonal.

	Feeding	Fat	Condition	Reproduction (GSR)
A. robertsi				
Feeding		-0.22	0.38*	-0.51**
Fat	-0.01		0.53**	0.04
Condition	0.44**	0.52**		-0.28
Reproduction (GSR)	-0.38*	-0.28	-0.70***	
H. microlepis				
Feeding		-0.27	0.35*	-0.26
Fat	-0.29		0.30*	0.27
Condition	0.30*	0.26		-0.01
Reproduction (GSR)	0.01	0.04	-0.21	
H. unimaculatus				
Feeding		-0.21	0.14	-0.51**
Fat	-0.47**		0.65***	-0.16
Condition	0.14	0.55***		-0.44**
Reproduction (GSR)	-0.28	-0.13	-0.54***	

with body condition and feeding activity, whereas body condition correlated positively with feeding activity and fat storage (Table 3). Regarding males, reproductive effort correlated negatively with feeding activity, while body condition correlated positively with feeding activity and fat (Table 2). *Argonectes robertsi* showed high similarity in diet between periods (Pianka's index = 0.85), consuming basically invertebrates, detritus/sediment and vegetal (Table 4). After the impoundment, however, we registered an increase in the consumption of vegetal and a decrease in terrestrial insects.

Hemiodus microlepis

In Pre-impoundment periods, *H. microlepis* was captured mainly in upper sites; after the impoundment, most fish were captured in upper and transitional sites of the reservoir (Fig. 1). This species presented significant changes, for both sexes, in feeding activity (Kruskall-Wallis, $H_{female} = 31.5$; $p < 0.00001$; $H_{male} = 62.1$; $p < 0.00001$), fat storage ($H_{female} = 475.0$; $p < 0.0001$; $H_{male} = 396.2$; $p < 0.0001$), body condition ($H_{female} = 442.7$; $p < 0.0001$; $H_{male} = 428.3$; $p < 0.0001$) and reproductive effort ($H_{female} = 84.2$; $p < 0.00001$; $H_{male} = 219.2$; $p < 0.0001$) between Pre and Post-impoundment periods. We recorded higher values of fat storage and body condition in Post-1, whereas feeding activity tended to decrease in Post-2 (Fig. 3). Reproductive effort also showed considerable variation among periods, reducing for females and increasing for males (Fig. 3). We registered, for females, a significant positive correlation between feeding activity and body condition; for males, body condition correlated positively with feeding activity and fat storage (Table 3). *Hemiodus microlepis* also showed high diet similarity between periods (Pianka's index = 0.86), consuming basically sediments/detritus and algae; with reduction in the consumption of vegetal after the impoundment (Table 4).

Hemiodus unimaculatus

In Pre-impoundment periods, *H. unimaculatus* was captured mainly in upper sites; after the impoundment, most captures occurred in the Transition and Lacustrine zones of the reservoir (Fig. 1). This species also showed significant changes, for both sexes, in feeding activity (Kruskall-Wallis, $H_{female} = 108.4$; $p < 0.0001$; $H_{male} = 44.6$; $p < 0.00001$), fat storage ($H_{female} = 764.0$; $p < 0.0001$; $H_{male} = 253.0$; $p < 0.0001$), body condition ($H_{female} = 393.8$; $p < 0.0001$; $H_{male} = 314.9$; $p < 0.0001$) and reproductive effort ($H_{female} = 61.9$; $p < 0.00001$; $H_{male} = 197.8$; $p < 0.0001$) between Pre and Post-impoundment periods. Higher values of fat storage and body condition were recorded in post-impoundment periods (Fig. 4), while feeding activity tended

Table 4. Feeding resources (occurrence and volume, %) consumed by *A. robertsi*, *H. microlepis*, and *H. unimaculatus*, before and after the construction of Lajeado Reservoir. N = 12 fish/period for each species. Occ = ?; Vol. = ?

Resources	*A. robertsi*				*H. microlepis*				*H. unimaculatus*			
	Pre		Post		Pre		Post		Pre		Post	
	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.	Occ.	Vol.
Algae	0.0	0.0	0.0	0.0	100	20	100	14.4	90.9	32.3	91.7	22.6
Sediment/Detritus	66.7	5.6	91.7	9.9	100	50	100	84.3	90.9	36.3	100	67.9
Aquatic insects	100	54.9	100	71.0	8.3	0.1	25.0	0.3	27.3	8.7	16.7	0.8
Terrestrial insects	66.7	39.2	83.3	5.6	8.3	0.1	16.7	0.1	27.3	21.3	33.3	3.8
Microcrustaceans	0.0	0.0	8.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	25.0	2.7
Other invertebrates	0.0	0.0	8.3	4.7	16.7	0.2	0.0	0.0	9.1	0.1	33.3	0.0
Vegetal	8.3	0.3	91.7	8.5	100	29.6	8.3	0.9	27.3	1.3	33.3	2.1

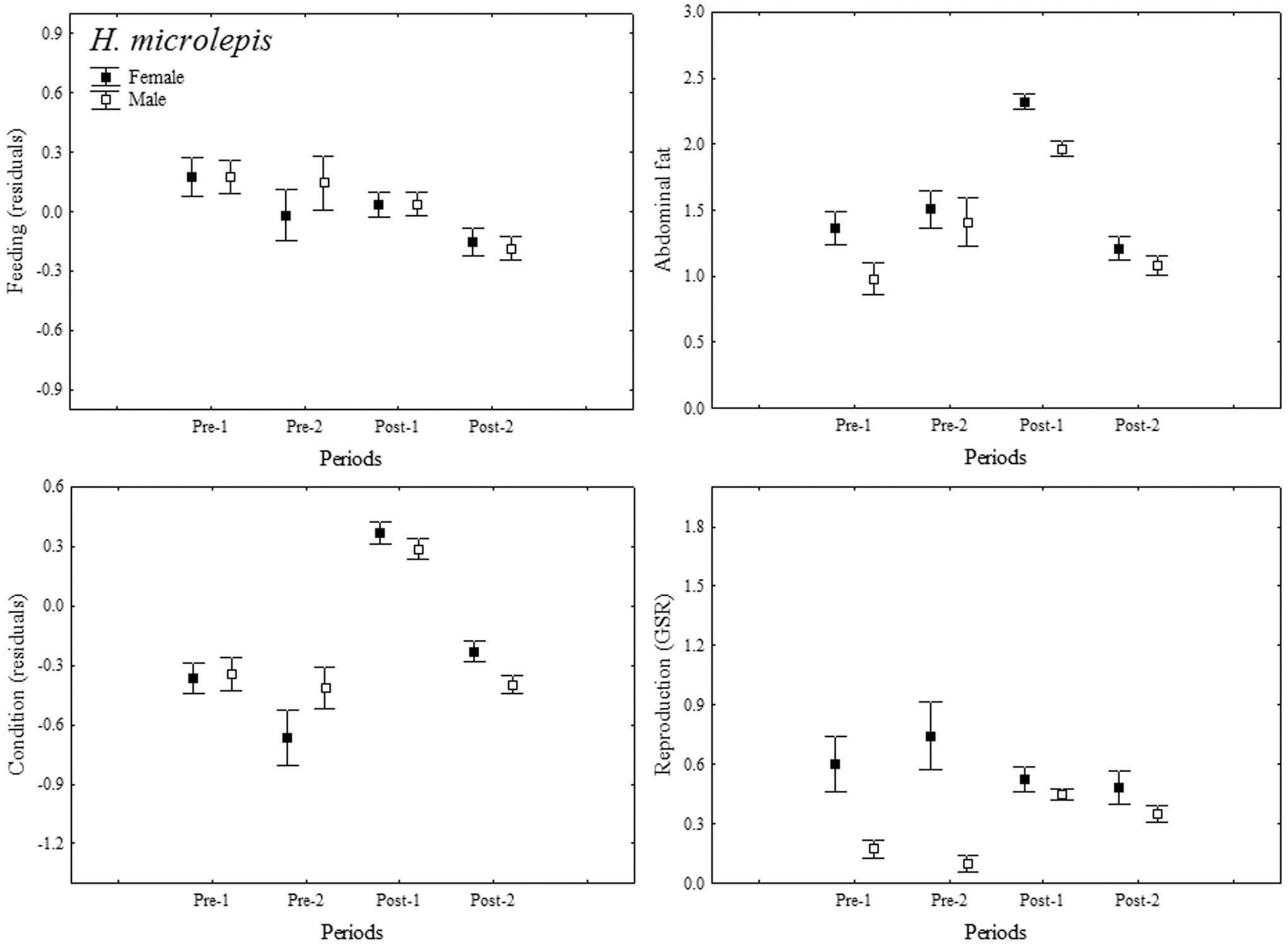

Fig. 3. Variation in feeding activity (standard residuals, regression between LS x WS), visceral fat storage, body condition (standard residuals, regression between LS x TW) and reproductive effort (GSR) of *Hemiodus microlepis*, before (Pre-1 and 2) and after (Post-1 and 2) the construction of Lajeado Dam.

to reduce, particularly for females. In addition, as observed for *H. robertsi*, reproductive effort and its associated variability (IC 95%) decreased significantly after the impoundment (Fig. 4). For females, fat storage correlated negatively with feeding activity and positively with body condition; this last variable showed a negative correlation with reproductive effort (Table 3). For males, reproductive effort had a negative correlation with feeding activity and body condition; this last variable correlated positively with fat storage (Table 3). *Hemiodus unimaculatus* also presented little variation in diet between periods (Pianka's index = 0.85), consuming basically algae, sediments/detritus and invertebrates; with reduction in the ingestion of insects after the impoundment (Table 4).

Discussion

After the formation of Lajeado Reservoir, Tocantins River, we recorded significant variation in some ecological traits of Hemiodontidae fish, especially body condition and reproductive effort. In general, there was a decrease in reproductive activity after the impoundment, while visceral fat storage and body condition increased. These results clearly indicate that the impoundment changed energy allocation patterns between growth/maintenance and reproduction; in the case, after the impoundment, fish tended to allocate energy mainly to somatic processes.

Changes in energy allocation, with intensification of somatic activities, were clear for *A. robertsi* and *H. unimaculatus*, species that occupied the lentic areas of the reservoir. In the first years after the impoundment, we recorded reductions in reproductive activity for both species, while visceral fat and body mass increased consistently. The suppression of reproduction must have caused these alterations, considering that reproduction activities demand much energy (Okuda, 2001; McBride *et al.*, in press). In natural regimes, gonad maturation and behavioral aspects cause a significant consumption of energy reserves, such as lipid tissues (Adams & Huntingford, 1997; Arrington *et al.*, 2006), which are restored between

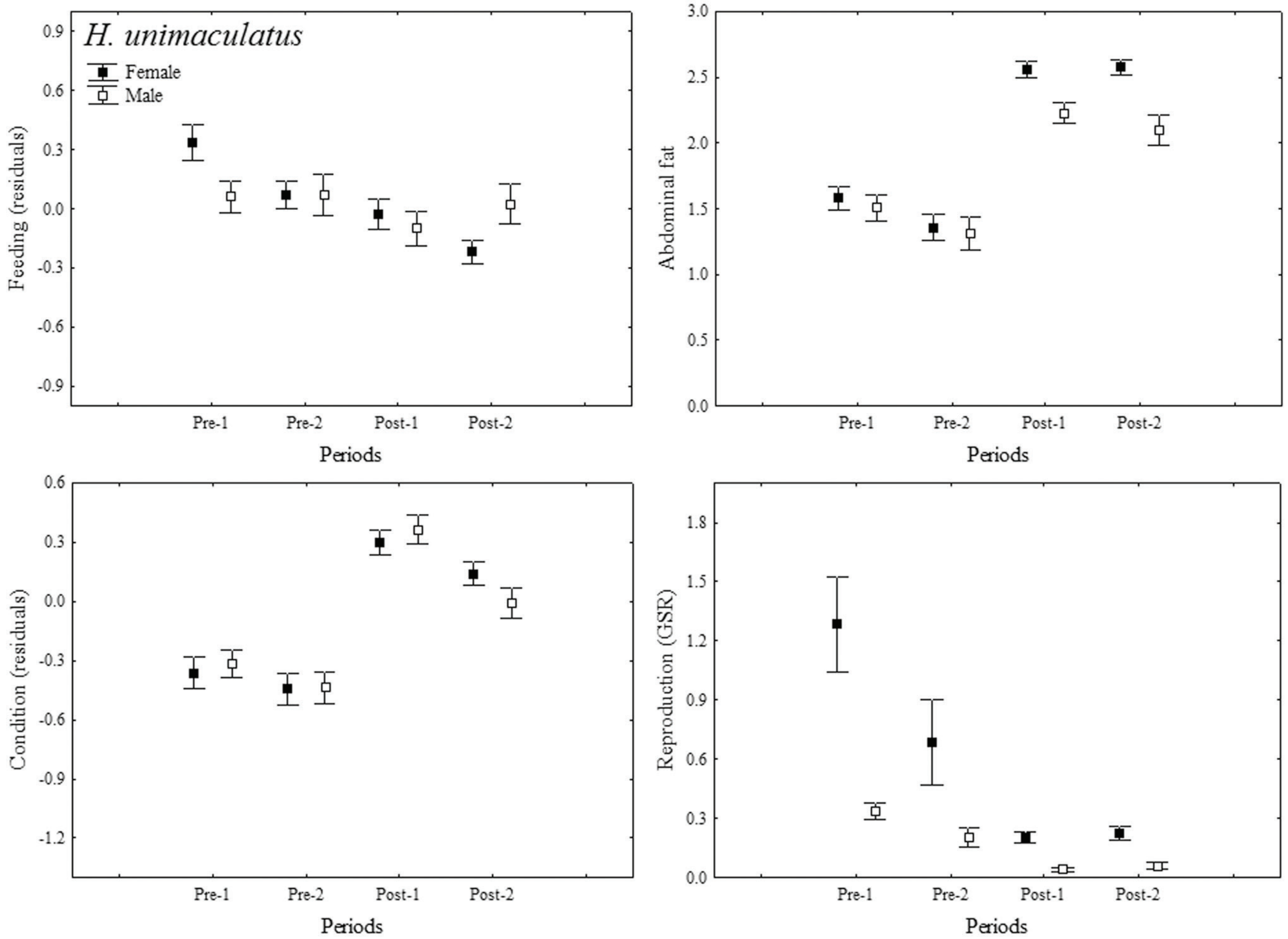

Fig. 4. Variation in feeding activity (standard residuals, regression between LS x WS), visceral fat storage, body condition (standard residuals, regression between LS x TW) and reproductive effort (GSR) of *Hemiodus unimaculatus*, before (Pre-1 and 2) and after (Post-1 and 2) the construction of Lajeado Dam.

breeding seasons. Alternatively, changes in allocation patterns could be explained by changes in feeding activity (*i.e.*, intensity) and diet, since energy sources may be extensively replaced after the impoundment. However, it seems not the case, considering that *A. robertsi* exhibited higher feeding activity after the impoundment, whereas *H. unimaculatus* decreased activity. In addition, all species showed little variation in diet, consuming the same resources in pre and post-impoundment periods. We emphasize also that *H. microlepis*, which showed less marked changes in reproductive effort, also showed less conspicuous variation in body condition and fat storage. In terms of metabolism, therefore, the suppression of seasonal reproductive dynamics must have canalized energy to somatic activities, such as growth, maintenance and/or storage.

We highlight that these species have not adopted a new strategy to allocate energy in response to the impoundment; we believe they are simply responding to disturbances provoked in reproductive traits. Hemiodontidae fish are medium-sized, iteroparous and rheophylic, they can perform reproductive migration, reproduce seasonally during the rainy period and present total spawning type (Brandão *et al.*, 2003; Medeiros *et al.*, 2009; Neuberger *et al.*, 2009). Species with such life history traits, what include many South American fish species, respond to specific environmental triggers (proximal factors) that stimulate the reproductive cycle - including migration, gonadal maturation and spawning (Vazzoler, 1996; Agostinho *et al.*, 2004; Bailly *et al.*, 2008). When rivers are regulated, however, such triggers are severely changed, including alterations in the flow regime and water quality (Agostinho *et al.*, 2004). In the present case, stimulus related to gonadal development (*e.g.*, rising water level) were probably absent in the years that followed river impoundment, considering that very low GSR values were recorded in post-impoundment periods, for both males and females. In addition, the high variability in GSR values (IC 95%) registered before river regulation suggests that gonadal development was variable within years (seasonal), tracking variations in environmental settings. These patterns (*i.e.*, seasonal reproduction in natural conditions; absence of reproduction after damming) were also observed for Hemiodontidae fish in Peixe Angical Reservoir (Medeiros *et al.,* 2009), located immediately upstream Lajeado Dam. Reservoir environments, therefore, lack the factors that trigger the reproductive cycle, preventing fish to allocate energy to such process. We highlight that species that showed clear alteration in energy allocation patterns (*H. unimaculatus* and *A. robertsi*) were captured mainly in lentic sites after the impoundment - a region more affected by the impoundment (Araújo *et al.*, 2013).

The ecological consequences that may follow must be well understood, because changes in energy allocation create the false impression that healthier fish are found in reservoirs. In fact, "fat" fish, with increased body condition, have been commonly observed in different impoundments in Brazil - including migratory species, which seem to reside, for long periods, in sites close to the dam (F. M. P. & C. S. A., pers. obs.). Such increased body mass, obviously, will not translate into population recruitment, basically because it is the outcome of failures in reproduction; in the case, better individual condition will not translate into increased individual fitness. We can predict, therefore, that the dominance of somatic processes may have negative effects on the persistence of fish populations in Lajeado Reservoir, unless Hemiodontidae fish adjust their reproductive tactics to the new conditions in next years. In Itaipu Reservoir, Paraná River, for example, many species presented the first evidences of reproduction only after the fourth year of impoundment (Agostinho *et al.*, 2007). A possibility of population persistence is the use of areas located upstream, where recruitment may ensue. There is a relevant fluvial segment between Lajeado and Peixe Angical Dam, with the presence of tributaries and small floodplains (Agostinho *et al.*, 2011; Araújo *et al.*, 2013). In this case, the impoundment may work as feeding and/or residence site, while remnant lotic stretches and associated environments work as spawning grounds and nursery. Similar dynamics were recorded in Itaipu Reservoir, where species with different life-history patterns (including the migratory *Prochilodus lineatus*) use the reservoir as a feeding site, but reproduce in lotic areas located upstream (Agostinho *et al.*, 2007). Considering that Hemidontidae species are common in Amazonian impoundments (Santos, 1995; Santos *et al.*, 2004), we believe that these fish will colonize Lajeado Reservoir in next years, using remnant riverine environments to complete their life cycle. Further studies are needed to confirm the persistence of populations in the area, and to reveal demographic consequences that may follow from recruitment failures in the first years of impoundment (*e.g.*, absence of cohorts).

Many studies have reported alterations in the structure of fish populations and communities after river regulation (*e.g.*, synthesis in Agostinho *et al.*, 2007); some investigations, in particular, claim that many Neotropical species are not able to sustain populations in areas affected by impoundments (Gomes & Miranda, 2001; Oliveira *et al.*, 2005; Terra & Araújo, 2010; Petesse & Petrere Jr., 2012; Araújo *et al.*, 2013). Hypotheses have been proposed to explain these changes, including changes/losses of feeding resources, habitats and particular environmental settings that are important to specific life history stages (Agostinho *et al.*, 2007). Although a multi-causal or even species-specific context must be evoked to explain ecological changes caused by dams, the present study identified a specific biological mechanism, showing that the impoundment disturbed the reproductive cycle of Hemodontidae fish, with immediate changes in energy allocation patterns. As a consequence, changes in energy allocation patterns produced fish with greater somatic condition, but with decreased fitness. Failures in reproduction, in this sense, probably represent a significant bottleneck for the colonization and persistence of fish populations in large reservoirs.

Acknowledgments

We thank colleagues from the Núcleo de Estudos Ambientais (Universidade Federal do Tocantins) for their assistance in field and laboratory work. We also thank Investco S.A. for financial support. Comments provided by two anonymous reviewers improved considerably the manuscript. CNPq provided a scholarship for E.R.M. and a research grant for F.M.P.

Literature Cited

Abujanra, F., A. A. Agostinho & N. S. Hahn. 2009. Effects of the flood regime on the body condition of fish of different trophic guilds in the Upper Paraná River floodplain, Brazil. Brazilian Journal of Biology, 69: 469-479.

Adams, C. E. & C. E. Huntingford. 1997. Growth, maturation and reproductive investment in Arctic charr. The Fisheries Society of the British Isles. Journal of Fish Biology, 51: 750-759.

Agostinho, A. A., L. C. Gomes, V. Samuel & E. K. Okada. 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.

Agostinho, A. A., L. C. Gomes & F. M. Pelicice. 2007. Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. Maringá, Eduem.

Agostinho, A. A., F. M. Pelicice & L. C. Gomes. 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Brazilian Journal of Biology, 68: 1119-1132.

Agostinho, C. S., F. M. Pelicice, E. E. Marques, A. B. Soares & D. A. A. Almeida. 2011. All that goes up must come down? Absence of downstream passage through a fish ladder in a large Amazonian river. Hydrobiologia, 675: 1-12.

Araújo, E. S., E. E. Marques, I. S. Freitas, A. L. Neuberger, R. Fernandes & F. M. Pelicice. 2013. Changes in distance decay relationships after river regulation: similarity among fish assemblages in a large Amazonian river. Ecology of Freshwater Fish, 22: 543-552.

Arrington, D. A., B. K. Davidson, K. O. Winemiller & C. A. Layman. 2006. Influence of life history and seasonal hydrology on lipid storage in three Neotropical fish species. Journal of Fish Biology, 68: 1347-1361.

Bailly, D., A. A. Agostinho & H. I. Suzuki. 2008. Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. River Research and Applications, 24: 1218-1229.

Ballón, M., C. Wosnitza-Mendo, R. Guevara-Carrasco & A. Bertrand. 2008. The impact of overfishing and El Niño on the condition factor and reproductive success of Peruvian hake, *Merluccius gayi peruanus*. Progress in Oceanography, 79: 300-307.

Benedito-Cecílio, E., A. L. Pereira & C. M. Sakuragui. 2004. Effect of size on the energy acquired in species of the fish from a neotropical reservoir, Brazil. Environmental Biology of Fishes, 71: 313-320.

Brandão, C. A. S., M. F. M. Valentim & E. P. Caramaschi. 2003. Ovary maturation stages and oocyte features in three species of the Netropical fish *Hemiodus* (Muller, 1842). Brazilian Archives of Biology and Technology, 46: 433-441.

Davis, A. M., M. L. Blanchette, B. J. Pusey, T. D. Jardine & R. G. Pearson. 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. Freshwater Biology, 57: 2156-2172.

Gomes, L. C. & L. E. Miranda. 2001. Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the Upper Paraná River Basin. Regulated Rivers: Research & Management, 17: 67-76.

Gotelli, N. J. & G. L. Entsminger. 2001. EcoSim: Null models software for ecology, Version 7.2. Acquired Intelligence Inc. & Kesey-Bear. Available from: http:// http://garyentsminger.com (September 2013).

Heino, M. & V. Kaitala. 1999. Evolution of resource allocation between growth and reproduction in animals with indeterminate growth. Journal of Evolutionary Biology, 12: 423-429.

Hoeinghaus, D. J., K. O. Winemiller, C. A. Layman, D. A. Arrington & D. B. Jepsen. 2006. Effects of seasonality and migratory prey on body condition of *Cichla* species in a tropical floodplain river. Ecology of Freshwater Fish, 15: 398-407.

Loureiro-Crippa, V. E. & N. S. Hahn. 2006. Use of food resources by the fish fauna of a small reservoir (rio Jordão, Brazil) before and shortly after its filling. Neotropical Ichthyology, 4: 357-362.

Lucinda, P. H. F., I. S. Freitas, A. B. Soares, E. E. Marques, C. S. Agostinho & R. J. Oliveira. 2007. Fish, Lajeado Reservoir, rio Tocantins drainage, State of Tocantins, Brazil. Check List, 3: 70-83.

Luz-Agostinho, K. D. G., L. M. Bini, R. Fugi, A. A. Agostinho & H. F. Júlio Jr. 2006. Food spectrum and trophic structure of the ichthyofauna of Corumbá reservoir, Paraná river Basin, Brazil. Neotropical Ichthyology, 4: 61-68.

McBride, R. S., S. Somarakis, G. R. Fitzhugh, A. Albert, N. A. Yaragina, M. J. Wuenschel, A. Alonso-Fernandez & G. Basilone. (in press). Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish and Fisheries.

Medeiros, E. R., A. L. Neuberger & C. S. Agostinho. 2009. Variações sazonais na atividade reprodutiva de peixes na área de influência do reservatório de Peixe Angical. Pp. 69-76. In: Agostinho, C. S., F. M. Pelicice & E. E. Marques (Orgs.). Reservatório de Peixe Angical: Bases ecológicas para o manejo da ictiofauna. São Carlos, RiMa Editora.

Mérona, B., G. M. Santos & R. G. Almeida. 2001. Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities. Environmental Biology of Fishes, 60: 375-392.

Mérona, B., R. Vigouroux & V. Horeau. 2003. Changes in food resources and their utilization by fish assemblages in a large tropical reservoir in South America (Petit-Saut Dam, French Guiana). Acta Oecologica, 24: 147-156.

Mérona, B., A. A. Juras, G. M. Santos & I. H. A. Cintra. 2010. Os peixes e a pesca no baixo rio Tocantins: vinte anos depois da UHE Tucurui. Brasília, Eletrobrás, Eletronorte.

Neuberger, A. L., E. E. Marques, C. S. Agostinho & F. M. Pelicice. 2009. Variações espaciais na atividade reprodutiva de peixes na área de influência do reservatório de Peixe Angical. Pp. 59-68. In: Agostinho, C. S., F. M. Pelicice & E. E. Marques (Orgs.). Reservatório de Peixe Angical: bases ecológicas para o manejo da ictiofauna. São Carlos, RiMa Editora.

Okuda, N. 2001. The costs of reproduction to males and females of a paternal mouthbrooding cardinal fish *Apogon notatus*. Journal of Fish Biology, 58: 776-787.

Oliveira, E. F., C. V. Minte-Vera & E. Goulart. 2005. Structure of fish assemblages along spatial gradients in a deep subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay border). Environmental Biology of Fishes, 72: 283-304.

Pelicice, F. M. & A. A. Agostinho. 2008. Fish passage facilities as ecological traps in large Neotropical Rivers. Conservation Biology, 22: 180-188.

Peressin, A., C. S. Gonçalves & F. M. S. Braga. 2012. Reproductive strategies of two Curimatidae species in a Mogi Guaçu impoundment, upper Paraná River basin, São Paulo, Brazil. Neotropical Ichthyology, 10: 847-854.

Petesse, M. L., M. Petrere Jr. 2012. Tendency towards homogenization in fish assemblages in the cascade reservoir system of the Tiete river basin, Brazil. Ecological Engineering, 48: 109-116.

Santos, G. M. 1995. Impactos da hidrelétrica Samuel sobre as comunidades de peixes do rio Jamari (Rondônia - Brasil). Acta Amazônica, 25: 247-280.

Santos, G. M., B. Mérona, A. A. Juras & M. Jégu. 2004. Peixes do Baixo Tocantins: 20 anos depois da Usina Hidrelétrica de Tucuruí. Brasília, Eletronorte.

Santos, R. N., S. Amadio & E. J. G. Ferreira. 2010. Patterns of energy allocation to reproduction in three Amazonian fish species. Neotropical Ichthyology, 8: 155-162.

Soares, A. B., F. M. Pelicice, P. H. F. Lucinda, A. Akama & C. S. Agostinho. 2009. Diversidade de peixes na área de influência da barragem de Peixe Angical, antes e após a formação do reservatório. Pp. 15-27. In: Agostinho, C. S., F. M. Pelicice & E. E. Marques (Orgs.). Reservatório de Peixe Angical: Bases ecológicas para o manejo da ictiofauna. São Carlos, RiMa Editora.

Statsoft, 2005. Statistica (data analysis software system). Version 7.1, StatSoft Inc., Tulsa.

Terra, B. F., A. B. I. Santos & F. G. Araújo. 2010. Fish assemblage in a dammed tropical river: an analysis along the longitudinal and temporal gradients from river to reservoir. Neotropical Ichthyology, 8: 599-606.

Vazzoler, A. E. A. M. 1996. Biologia da reprodução de peixes teleósteos: teoria e prática. Maringá, EDUEM.

Walsh, S. M., S. L. Hamilton, B. I. Ruttenberg, M. K. Donovan & S. A. Sandin. 2012. Fishing top predators indirectly affects condition and reproduction in a reef-fish community. Journal of Fish Biology, 80: 519-537.

Submitted October 15, 2013

Accepted January 9, 2014 by Norma S. Hahn

Published September 30, 2014