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Difference in reproduction energy content in muscles on fish from reservoirs in Paraná State, Brazil

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The variation in energy in the muscles of the most representative fish species from three Neotropical Reservoirs was investigated to determine the effect of the reproductive process on the amount of energy allocated and a possible relationship between the general welfare of the species and their caloric content. Significant differences were detected between the sexes and among the stages of gonad maturity. In general, the variation in energy in the muscles indicate to be a function of the reproductive cycle. In most examined species, females presented the highest caloric values, reflecting physiological differences in their use of energy, relative to the reproductive process. However, there was no significant correlation between caloric values and the condition factor of any species. Significant differences in the caloric content and condition factor were identified in each species belonging different trophic groups, indicating an effect of food quality on the amount of energy stored in the muscles. We conclude that the analyzed species presented a similar pattern of variation in energy, but that this was not reflected in their condition. In addition, an effect of reproduction and feeding habit on energy allocation was observed in both sexes.

Foi investigada a variação da energia nos músculos das espécies de peixes mais representativas de três reservatórios neotropicais, para determinar o efeito do processo reprodutivo na quantidade de energia alocada e uma possível relação entre o bem-estar geral das espécies e seu conteúdo calórico. Foram detectadas diferenças significativas entre os sexos e os estádios de maturidade gonadal. Em geral, a variação da energia nos músculos demonstra ser dependente do ciclo reprodutivo. Na maioria das espécies estudadas, as fêmeas apresentaram os maiores valores calóricos, refletindo as diferenças fisiológicas no uso de sua energia, em relação ao processo reprodutivo. No entanto, não houve correlação significativa entre os valores calóricos e o fator de condição as espécies estudadas. Diferenças significativas do conteúdo calórico e no fator de condição foram identificadas em cada espécie pertencente aos diferentes grupos trófcos, indicando um efeito de qualidade alimentar sobre a quantidade de energia armazenada nos músculos. Conclui-se que as espécies analisadas apresentaram um padrão semelhante de variação de energia, mas que isso não se refletiu em sua condição. Além disso, um efeito da reprodução e hábito alimentar, sobre a alocação de energia, foi observado em ambos os sexos.

Key words: Calorimetry, Condition factor, Freshwater fish, Paraná River basin, Trophic groups.

Introduction

One of the metabolic conflicts faced by an organism is whether to use its resources for biomass production (somatic or reproductive growth) or to meet the costs of maintenance activity (Calow, 1985; Kaspari *et al*., 2000; Hendry *et al*., 2001). In fish, the accumulation of caloric content and the patterns of allocation to metabolism, growth, and reproduction are essential for ecological success, mainly for those species that use energy reserves for migration and reproduction (Saldaña & Venables, 1983; Nurnadia *et al*., 2011). This process of energy allocation can be influenced by the consumption of food, environmental conditions, and changes in the reproductive cycle (Pandian & Vivekanandan, 1985). Several studies have shown seasonal differences in the caloric content of fish (Pandian & Vivekanandan, 1985; Berg & Bremset, 1998; Pedersen & Hislop, 2001; Arim *et al*., 2007). These variations are usually associated with the reproductive cycle, feeding, and storage of energy reserves, which tend to be more noticeable as the individual becomes larger and reaches sexual maturity (Tytler & Calow, 1985).

The pattern of caloric content allocation may differ according to the maturity of the individual, since reproductive activity as well as gonadal maturation imply the use of reserves obtained from food intake and from energy reserves deposited in different parts of the body, and in some cases

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may lead to a decrease in metabolic processes and somatic production (Tytler & Calow, 1985). Changes characteristics of the water (quantity and quality of food resources available to the fish) produced by flood pulses or the reservoirs may cause alterations in the welfare of the fish. These alterations can be quantified by the condition factor (Abujanra *et al*., 2009; Espínola *et al*., 2012). Variations in the condition factor (relationship between extrinsic and intrinsic variables and physiology of fish) and the caloric content of fish species have been used as indicators of physiological status and of changes in body composition (Encina & Granado-Lorencio, 1997; Paul *et al*., 1998). Different species present variations in accumulation and use of the caloric content. Thus these variations depend on habitat conditions, trophic category, food quality, and specific reproductive strategy (Huntingford *et al*., 2001; Fiorin *et al*., 2007). In general, studies that measure the caloric content have been used to quantify the energy used for reproduction (Huntingford *et al*., 2001; Jonsson & Jonsson, 2005). On the other hand, other studies have shown how fish use the caloric content accumulated in the muscles in environments with seasonal variations in the water level (Junk, 1985; Huss *et al*., 2008).

Studies on how the energy allocation is distributed into growth and survival, and how accumulated energy reserves vary according to seasonal environments in young fish, have been conducted experimentally in lakes and under simulated environmental conditions in aquaria respectively (Bryan *et al*., 1996; Post & Parkinson, 2001; Huss *et al*., 2008). Some studies were developed in natural freshwater systems (Glebe & Leggett, 1981) and others have been performed in marine environments (Pedersen & Hislop, 1981; Tirelli *et al*., 2006).

Despite the importance of studies on the energetic ecology of fish, few such studies have been performed in Brazil, and most have been performed on marine species (Ngan *et al*., 1993). For freshwater environments, some studies have been developed in the upper Paraná River floodplain (Doria & Andrian, 1997; Penczak *et al*., 1999; Benedito-Cecilio & Morimoto, 2002; Vismara *et al*., 2004; Rezende *et al*., 2008; Garcia *et al*., 2010, Espínola *et al*., 2012).

Espínola *et al*. (2008, 2010) examined the variation of the energetic content for two species of the Manso Reservoir, but the analyses relating to the energetic quantification of fish species have not yet been conducted between dammed environments. Consequently, studies that quantify energy allocation in fish populations in impounded environments will enable quantification of the energy available in these ecosystems, providing support for more efficient monitoring. Therefore, this study investigated the energy variation in the main fish species from three reservoirs of Paraná State, with the aim of addressing the following questions: i) Does reproduction affect energy allocation in fish in different trophic groups? ii) Do males and females show similar energy variation during gonadal maturation? iii) Is the energy stored in the muscles correlated with the general welfare of the fish species?

Material and Methods

Study areas. Sampling was conducted every three months between February and December 2002, in three reservoirs in Paraná State (Fig. 1), encompassing the rivers Iguaçu (Iraí and Segredo reservoirs) and Paranapanema (Rosana Reservoir).

Iraí Reservoir (25º25'10"S 49º06'49"W): this lies in the Iguaçu River basin, began operation in 1999, and is located between the municípios Quatro Barras and Piraquara, Pinhais. It covers 14.6 km^2, has a long residence time (> 1 year), and is relatively shallow (z_{max} = 8 m). In addition, it is considered to be one of the most eutrophic reservoirs in Paraná State (Júlio Jr. *et al.,* 2005).

Segredo Reservoir (25º47'28"S 52º07'36"W): this dam began operation in 1992, is the second in a series of four large reservoirs of the Middle Iguaçu River, and covers 80.6 km^2. It is located around 455 km from the mouth of the river, and 2 km upstream of the mouth of Jordão River. In the region surrounding the reservoir, the climatic conditions follow the same pattern described for the basin, with average annual rainfall of 1,900 mm, and no pronounced dry season (Júlio Jr. *et al*., 2005).

Rosana Reservoir (22º36'S 52º50'W): this is located in a stretch of the lower Paranapanema River, between the municípios Diamante do Norte (Paraná State) and Porto Primavera (São Paulo State), 25 km from the confluence with the Paraná River. It began operation in 1986, has an area of 220 km^2, and is 116 km long. The land use in the area affected by this dam consists mostly of agriculture, pasture, reforestation, and rural properties, corresponding to almost 80% of the area of the entire basin (Júlio Jr. *et al*., 2005).

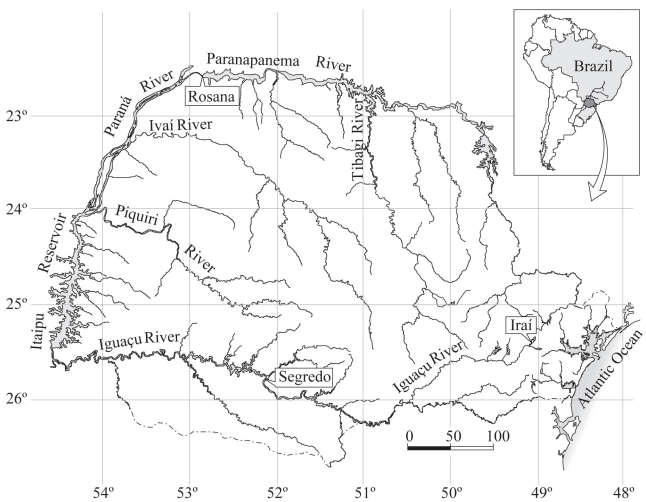

Fig. 1. Location of the reservoirs sampled in the present study, Paraná State.

Collection and data analysis. Sampling was conducted using gillnets of different mesh sizes (2.4 to 16 cm between opposing knots), left in place for 24 hours. The most representative species were selected for each reservoir, based on the CPUE (catch per unit effort), considering the number of captured individuals per 1,000 m^2 in 24 hours (Luiz *et al*., 2005). To estimate the calorie value per gram of dry weight, samples were taken from 615 individuals of abundant species belonging to the different trophic groups, according to Agostinho *et al.* (1997): Iraí - *Hoplias* aff. *malabaricus* (piscivore), *Astyanax minor* (detritivore), and *Geophagus brasiliensis* (invertivore); Segredo - *Apareiodon vittatus* (detritivore), *Corydoras* cf. *paleatus* (invertivore), and *Astyanax bifasciatus* (omnivore); Rosana - *Loricariichthys platymetopon* (detritivore), *Satanoperca pappaterra* (invertivore), and *Acestrorhynchus lacustris* (piscivore).

For each captured individual, data referring to standard length (SL) in centimeters, total weight (TW) in grams, sex, and gonad maturity stage were recorded. Macroscopic characters such as size, color, and vascularization, and visualization of oocytes, were used to determine the stages of maturity proposed by Vazzoler (1996). On average, eight individuals of each gonad maturity stage (resting - RES; early maturation - EMT; maturing - MAT; mature - MTE; and spent - SPT) were analyzed for each sex (males and females), but not all stages were available. The presence of the EMT stage was justified by the need to extend the stages of maturity to include gonads that have already started the maturation process and those that already have growing oocytes (Vazzoler, 1981). In some cases, these two stages can be combined, but in terms of energetic content, the EMT stage shows a very distinct trend from the other stages in all species in which it has been characterized, and it was thus analyzed separately.

From each specimen, we extracted muscle samples from the base of the dorsal fin, for both sexes and at each gonadal maturation stage. The table 2 shows the number for each sex and gonadal maturation stage. All the samples were preserved in ice and taken to the laboratory of Energetic Ecology of Nupelia, where they were processed. Each sample was rinsed in distilled water and dried at 60°C in forced ventilation oven to constant weight. The dried muscles were ground in a ball mill to obtain a fine powder. The caloric value of the sample (kcal * g-1 dry weight) was determined by bomb calorimetry (PARR 1261) (Benedito-Cecilio & Morimoto, 2002).

The physiological status of males and females was determined by the variation in the mean values of the condition factor (K), according to the equation: K = (total weight / standard length)*100 (Vazzoler, 1996). The parameter "b" was obtained for both sexes, by means of the regression between the standard length and total weight.

Considering that the assumptions of normality and homoscedasticity were not satisfied a Kruskal-Wallis test was applied to the data of caloric values (kcal/g) and condition factor (K) of males and females, for the different gonad maturity stages of fish species in three reservoirs. A Mann-Whitney test was employed for intraspecific comparisons of the caloric values and condition factor, considering that the samples were independents. Spatial variations in caloric values and condition factor for each trophic group were presented graphically and tested with help of Kruskal-Wallis test. Then we carried out box-whisker plots for depicting groups of numerical data through their medians, quartiles, minimum and maximum values. To identify a possible relationship between the caloric content and condition factor of the sampled individuals beyond that revealed by graphic inspection, the data were submitted to a linear correlation analysis (Zar, 1999). The analyses were performed with the support of the Statistica 7.0. The significance level adopted for all analyses was $p < 0.05$.

Results

There were significant differences in caloric values for each sexes, considering all different gonad maturity stages in each species analyzed. Nevertheless, only for some cases were the condition factor significantly different (Table 1).

Intraspecific comparisons of the caloric values of individuals at each stage of maturity revealed significant differences between sexes in most cases (Table 2). *G. brasiliensis*, *H.* aff. *malabaricus*, and *L. platymetopon* were the only species with significant differences between sexes during all stages. For the other species, from one to four maturity stages were significantly different in caloric values between males and females. *Acestrorhynchus lacustris* was the only species which showed no differences.

Individuals with early maturation of the gonads presented the lowest caloric values in the muscle. Likewise, specimens whose gonads were fully developed (mature stage - MTE) presented the highest caloric values in Iraí, Rosana and Segredo reservoirs (Table 2).

In both sexes of each species, the caloric values of the muscle increased significantly during gonadal development, achieving the highest mean at the stage of maximum reproduction and decreasing following the end of the reproductive period (Tables 1-2) and with significant values. Significantly differences caloric values and condition factor were observed between detritivorous, invertivorous, and piscivorous species ($p < 0.05$) in all studied reservoirs, for both sexes (Figs. 2-3). The caloric values were the highest in *A. minor* (detritivore), *A. bifasciatus* (omnivore), and *S. pappaterra* (invertivore), depending of studied reservoir (Fig. 2) while for condition factor the invertivore species presented the higher values in all reservoirs.

Table 1. Results of the Kruskal-Wallis test applied to the data of caloric values (kcal/g) and condition factor (K) of males and females, considering the different gonad maturity stages of fish species in three reservoirs in the Paraná State (Df_{sta} = degree of freedom of the gonad maturity stage; Df_{case} = degree of freedom of each case; H= Kruskal-Wallis test; *= significant difference).

Reservoir	Species	Sex	Variable	Df_{sta}	Df_{case}	H	p
IRAÍ	*Astyanax minor*	Female	kcal	4	59	47.63	0.00*
			K	4	59	2.78	0.50
		Male	kcal	4	45	31.29	0.00*
			K	4	45	6.55	0.70
	Geophagus brasiliensis	Female	kcal	3	32	24.61	0.00*
			K	3	32	17.17	0.00*
		Male	kcal	4	32	26.93	0.00*
			K	4	32	18.42	0.00*
	Hoplias aff. *malabaricus*	Female	kcal	4	19	12.30	0.00*
			K	4	19	3.00	0.55
		Male	kcal	3	26	14.25	0.00*
			K	3	26	9.13	0.02*
SEGREDO	*Astyanax bifasciatus*	Female	kcal	3	50	44.52	0.00*
			K	3	50	20.54	0.00*
		Male	kcal	3	48	41.96	0.00*
			K	3	48	15.12	0.01*
	Astyanax vittatus	Female	kcal	4	41	32.19	0.00*
			K	4	41	12.49	0.00*
		Male	kcal	4	37	26.96	0.00*
			K	4	37	16.79	0.01*
	Corydoras cf. *paleatus*	Female	kcal	3	37	32.19	0.00*
			K	3	37	1.77	0.62
		Male	kcal	3	35	31.12	0.00*
			K	3	35	9.12	0.02*
ROSANA	*Satanoperca pappaterra*	Female	kcal	3	17	11.33	0.01*
			K	3	17	1.64	0.64
		Male	kcal	4	23	17.86	0.01*
			K	4	23	16.68	0.01*
	Loricariichthys platymetopon	Female	kcal	4	34	31.20	0.00*
			K	4	34	3.33	0.50
		Male	kcal	3	29	22.97	0.00*
			K	3	29	2.08	0.55
	Acestrorhynchus lacustris	Female	kcal	3	24	7.3	0.04*
			K	3	24	10.18	0.12
		Male	kcal	4	27	19.10	0.00*
			K	4	27	5.79	0.20

Table 2. Results of the Mann-Whitney test applied on the values of caloric (Kcal/g) values of males and females of fish species, at different gonad maturity stages (Res = Resting; Emt = Early maturation; Mat = Maturing; Mte = Mature; Spt = Spent) from three reservoirs in the Paraná State. N_F = number of females analyzed; N_M = number of males analyzed; U = Mann-Whitney Test; Z(U) = standardized value of U; *= significant difference.

Reservoir	Species	Stage	Median		N_F	N_M	U	Z (U)	p
			Females	Males					
IRAÍ	*Astyanax minor*	Res	5.27	5.26	10	3	14	0.17	0.87
		Emt	5.21	5.25	6	2	0.11	2.55	0.01*
		Mat	5.32	5.35	23	20	22	2.67	0.01*
		Mte	5.36	5.38	10	10	10	3.02	0.00*
		Spt	5.26	5.25	10	10	174	0.45	0.00*
	Geophagus brasiliensis	Res	5.18	5.21	10	11	1.50	3.77	0.00*
		Emt	5.14	5.15	10	10	22	2.12	0.03*
		Spt	5.23	5.24	10	7	34.50	1.94	0.04*
	Hoplias aff. *malabaricus*	Res	5.15	5.13	8	10	28.00	1.07	0.02*
		Emt	5.05	5.02	2	6	10.00	0.43	0.04*
		Mat	5.18	5.16	5	6	4	0.71	0.03*
		Spt	5.16	5.12	2	4	0	2.84	0.00*
SEGREDO	*Astyanax bifasciatus*	Res	5.23	5.22	10	11	17.5	2.64	0.01*
		Mat	5.31	5.32	20	17	24	0.65	0.00*
		Mte	5.35	5.34	10	10	12.5	2.83	0.00*
		Spt	5.26	5.25	10	10	200.5	0.25	0.80
	Apareiodon vittatus	Res	5.21	5.21	2	2	4	1.15	0.25
		Emt	5.20	5.21	9	6	6	2.47	0.01*
		Mat	5.21	5.22	17	11	18	2.42	0.06
		Mte	5.24	5.22	3	10	0	2.54	0.01*
		Spt	5.20	5.21	10	8	69	0.40	0.69
	Corydoras cf. *paleatus*	Res	5.16	5.16	2	9	13	0.77	0.44
		Mat	5.21	5.21	15	12	8	0.49	0.62
		Mte	5.26	5.25	10	6	5.5	2.66	0.01*
		Spt	5.19	5.20	10	8	125	1.11	0.27
ROSANA	*Satanoperca pappaterra*	Res	5.21	5.20	2	3	0	2.12	0.03*
		Mte	5.24	5.24	2	2	4	1.15	0.25
		Spt	5.21	5.16	9	2	61.5	0.28	0.78
	Loricariichthys platymetopon	Res	5.15	5.17	10	10	2	3.63	0.00*
		Emt	5.10	5.05	5	15	0	3.27	0.00*
		Spt	5.13	5.14	8	3	32	1.00	0.00*
	Acestrorhynchus lacustris	Res	5.11	5.12	5	4	3.5	1.59	0.11
		Mte	5.14	5.14	12	11	62.5	0.22	0.83
		Spt	5.14	5.12	1	1	7	0.80	-

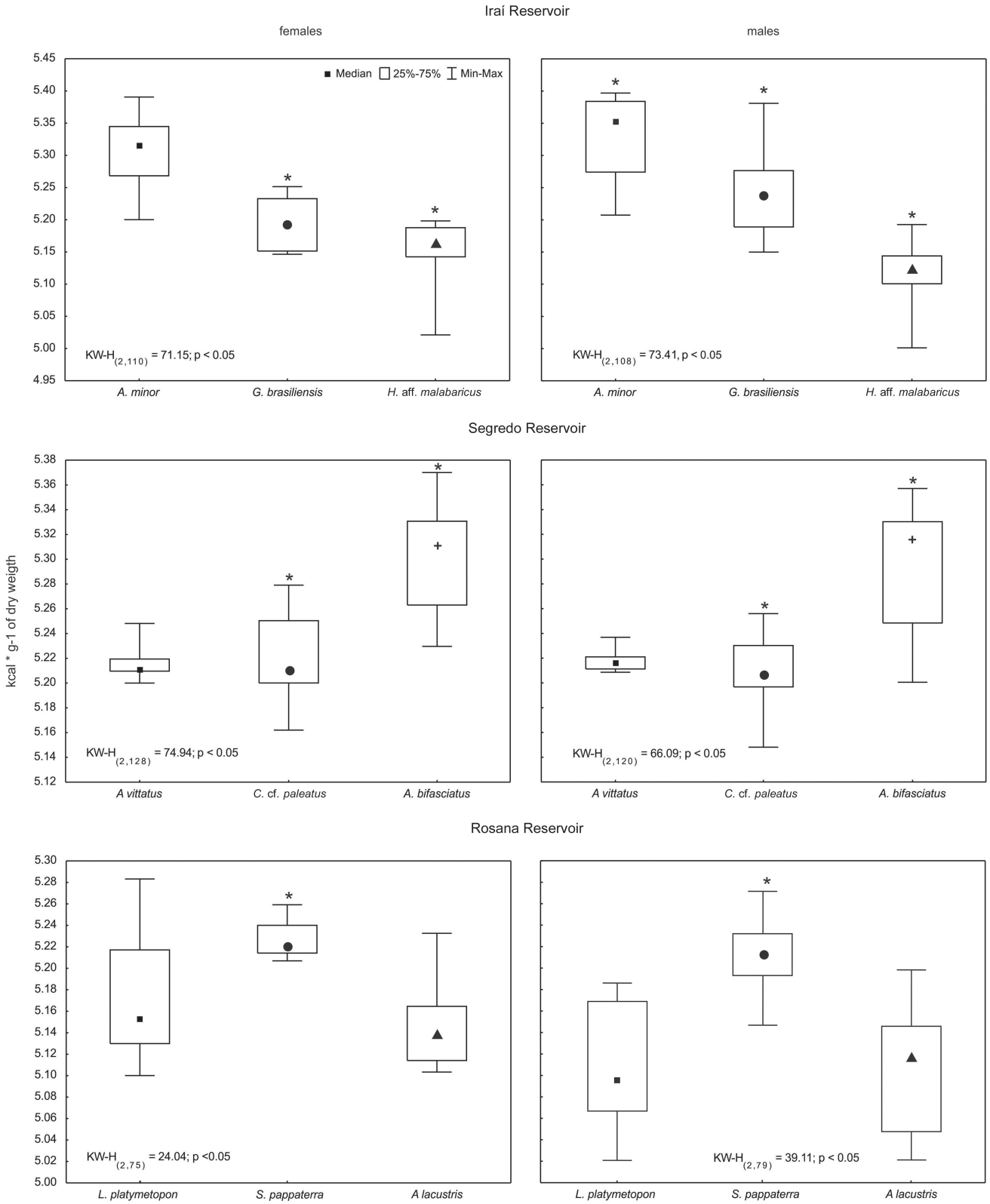

Fig. 2. Spatial variation (median, quartiles, maximum and minimum values) for caloric values in kcal * g-1 dry weight of males and females of *Acestrorhynchus lacustris*, *Apareiodon vittatus*, *Astyanax bifasciatus*, *Astyanax minor*, *Corydoras* cf. *paleatus*, *Geophagus brasiliensis*, *Hoplias* aff. *malabaricus*, *Loricariichthys platymetopon*, and *Satanoperca pappaterra* of different trophic groups (square - detritivorous, dot - invertivorous, triangle - piscivorous, cross - omnivorous) in three reservoirs in Paraná State (KW-H = values of H of Kruskal-Wallis test - *= significant difference).

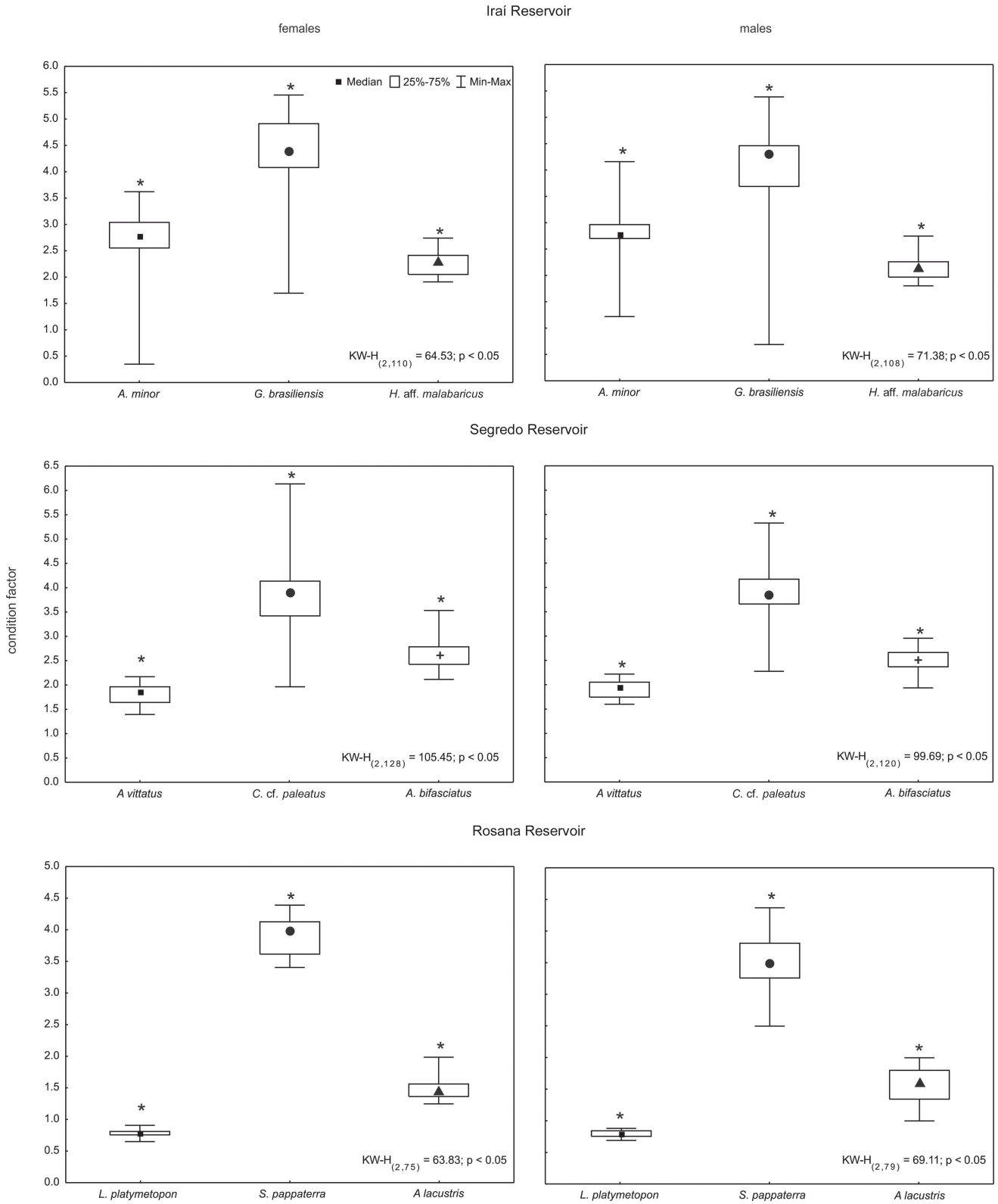

Fig. 3. Spatial variation (median, quartiles, maximum and minimum values) for condition factor of males and females of *Acestrorhynchus lacustris*, *Apareiodon vittatus*, *Astyanax bifasciatus*, *Astyanax minor*, *Corydoras* cf. *paleatus*, *Geophagus brasiliensis*, *Hoplias* aff. *malabaricus*, *Loricariichthys platymetopon*, and *Satanoperca pappaterra* of different trophic groups (square - detritivorous, dot - invertivorous, triangle - piscivorous, cross - omnivorous) in three reservoirs in Paraná State (KW-H = values of H of Kruskal-Wallis test - *= significant difference).

Moreover, there was no significant correlation between the condition factor and caloric values in all species examined in the present study.

Significant differences in condition factor between males and females were not found for any species from Rosana and Segredo reservoirs, except for *A. bifasciatus* from the latter reservoir. For *A. bifasciatus* and species from Iraí Reservoir differences were detected for only one gonad maturity stage (Table 3). These findings could indicate that the value of K varied depending on the sex and reservoir.

Table 3. Results of the Mann-Whitney test applied on the values of condition factor of males and females of fish species, at different gonad maturity stages (Res = Resting; Emt = Early maturation; Mat = Maturing; Mte = Mature; Spt = Spent) from three reservoirs in the Paraná State. N_F = number of females analyzed; N_M = number of males analyzed; U = Mann-Whitney Test; Z(U) = standardized value of U; *= significant difference.

Reservoir	Species	Stage	Median		N_F	N_M	U	Z(U)	p
			Females	Males					
IRAÍ	*Astyanax minor*	Res	2.62	2.78	10	3	13.50	-0.25	0.79
		Emt	2.83	2.97	6	2	4	-0.66	0.55
		Mat	2.79	2.76	23	20	218	0.29	0.77
		Mte	2.85	2.79	10	10	31	1.43	0.15
		Spt	2.70	3.15	10	10	22	-2.11	0.03*
	Geophagus brasiliensis	Res	4.61	4.13	10	11	20	0.46	0.01*
		Emt	4.84	4.64	10	10	43	0.52	0.59
		Spt	3.98	3.42	10	7	22	1.26	0.20
	Hoplias aff. *malabaricus*	Res	2.04	2.20	8	10	31	-0.79	0.42
		Emt	2.37	1.95	2	6	0	2.00	0.04*
		Mat	2.31	12.25	5	6	9	1.09	0.27
		Spt	2.42	2.23	2	4	3	0.46	0.64
SEGREDO	*Astyanax bifasciatus*	Res	2.27	2.35	10	11	49	-0.42	0.67
		Mat	2.57	2.56	20	17	143	0.82	0.41
		Mte	2.80	2.71	10	10	23	2.04	0.04*
		Spt	2.48	2.42	10	10	34	1.20	0.22
	Astyanax vittatus	Res	1.94	1.82	2	2	2	0.00	1.00
		Emt	1.95	1.96	9	6	27	0.00	1.00
		Mat	1.69	1.71	17	11	78	-0.72	0.46
		Mte	1.71	2.02	3	10	9	-1.01	0.31
		Spt	1.81	2.03	10	8	18	-1.95	0.08
	Corydoras cf. *paleatus*	Res	3.19	3.87	2	9	8	-0.23	0.81
		Mat	3.96	3.90	15	12	88	0.09	0.92
		Mte	3.68	3.42	10	6	19	1.19	0.23
		Spt	3.92	3.84	10	8	37	-0.26	0.78
ROSANA	*Satanoperca papaterra*	Res	4.11	2.86	2	3	3	-1.83	0.40
		Mte	3.73	3.52	2	2	1	0.77	0.43
		Spt	3.99	3.67	9	2	5	0.94	0.34
	Loricariichthys platymetopon	Res	0.78	0.77	10	10	39	0.83	0.40
		Emt	0.76	0.77	5	15	27	-9.16	0.35
		Spt	0.79	0-83	8	3	7	-1.02	0.30
	Acestrorhynchus lacustris	Res	1.37	1.54	5	4	5	-1.22	0.22
		Mte	1.50	1.51	12	11	50	-0.98	0.32
		Spt	1.75	1.80	1	1	1	-1.34	-

Discussion

Significant differences in caloric values were detected between the sexes. Females of many species use more of their energy reserves as they expend more energy during oocyte maturation, due to the production of larger gametes than in males (Vazzoler, 1996; Jonsson & Jonsson, 1998). However, an exception was observed in Iraí Reservoir where the males had more energy in their muscle tissue. This result may be associated with the reproductive tactics displayed by the species analyzed, especially when considering *A. minor* and *G. brasiliensis*. For the family of *G. brasiliensis*, the males present sexual dimorphism at the time of reproduction, involving small differentiating structures or even brightly colored patterns (Breder & Rosen, 1966). These characteristics demand energy and may be related to the high amount of energy recorded in the males from this reservoir.

The reproductive success of an organism is greatly influenced by how the available energy in its body is divided between somatic growth, gonadal development, and metabolic activities (Watt, 1986). In general, the pattern of energy in the muscles varied as a function of the reproductive cycle. Individuals in the early stages of maturation presented the lowest caloric content, with energy subsequently increasing during development. The maximum caloric values were achieved when the gonads were at the advanced stage of maturity, with a reduction after spawning. Prus (1970) reported that the highest caloric contents were observed during periods preceding food shortage or during reproduction. On the other hand, the amount of energy was lower until the start of the reproductive process in all species. This reduction may be related to spawning activity, which influenced the individuals for a longer period in comparison to other periods. It is possible that the impounded environment may impose limitations, both biotic and abiotic, that should be investigated in more detail in new studies.

Although the above-mentioned pattern was observed in most of the studied species, a different trend was observed in males of *H.* aff. *malabaricus* in Iraí Reservoir and of *L. platymetopon* in Rosana Reservoir, and also in females of *C.* cf. *paleatus* in Segredo Reservoir. In these three species, individuals with gonads at the resting stage showed an increase in energy after spawning, which was more pronounced in the latter two species. On the other hand, when analyzing the effect of gonadal maturation on the caloric content of fish species of the upper Paraná River floodplain, Vismara *et al*. (2004) observed the opposite trend in males of *L. platymetopon*. Moreover, the authors reported caloric densities for this species that were lower than those found in the present study, for both sexes (ranging from 4.65 to 5.15 kcal * g-1 dry weight in females, and 4.65 to 5.11 kcal * g-1 dry weight in males). In accordance with Abujanra *et al.* (2009), the retention of nutrients and sediment behind the Porto Primavera Dam upstream causes the dilution of nutrients and reduction in drifting food organisms, and it intensifies the effects of the floods on the body condition of the fish.

Hoplias aff. *malabaricus*, *L. platymetopon*, and *C.* cf. *paleatus* have split spawning, external fertilization, and parental care, respectively (Suzuki & Agostinho, 1997; Nakatani *et al*., 2001). Males of *H*. aff. *malabaricus* exhibit aggressive behavior when taking care of the nest, reacting to the presence of any potential predator (Querol *et al*., 2003). On the other hand, males of *L. platymetopon* have several genital papillae, under the lower lip, as accessory sexual characteristics, which are used to carry the egg mass (Nakatani *et al*., 2001). Thus rapid recovery of energy can be required to meet the expenses of behavioral aspects such as parental care.

According to Suzuki *et al*. (2000), split spawning requires a larger amount of energy for the process of gonadal maturation. During the resting stage, the gonads are prepared in order to start a new reproductive cycle, but in females of *C.* cf. *paleatus* it was found that the process of energy storage in the muscles began immediately after spawning. Thus, due to the intensification of this process, more energy may be stored in the muscles of females of this species for subsequent mobilization for reproduction.

The availability and quality of food are primary factors in the distribution of energy to different physiological processes in fish (Adams *et al*., 1982). Any factor altering the availability and quality of the food supply (density, abundance, and composition) will also change the energy input via changes in food intake, and consequently the entire allocation process. Significant differences were identified between species according to their feeding habits, indicating an effect of food quality on the amount of energy stored in the muscles. Lower numbers of calories per gram of dry weight were recorded for piscivorous species in the two environments in which they occurred. The highest caloric values varied between detritivores, omnivores and invertivores species, depending of reservoir analyzed. This fact indicates that the caloric values and composition of resources consumed were different in each reservoir. Odum (1988) stated that the amount of energy decreases along the trophic chain, but that the quality of the energy actually converted increases. In this way, as the amount of energy decreases, the quality of the energy in the trophic chain components increases, as observed for piscivores and invertivores. This species included higher quantity of animal organisms in its diet if compared to others trophic groups.

In the reservoirs with the highest nutrient concentrations (Iraí and Segredo), the species with the highest caloric content belonged to the genus *Astyanax* (*A. minor* and *A. bifasciatus*). These are considered to be opportunistic species, which show appropriate strategies in impacted environments such as reservoirs. In general, species of this genus are small and produce small oocytes, showing high relative fertility, rapid development, external fertilization, and no parental care - characteristics that enable them

to rapidly colonize these environments (Agostinho *et al*., 1999). In addition, when analyzing the reproductive characteristics of these species in reservoirs from the Iguaçu River basin, Bailly *et al*. (2005) recorded higher values of RGS (gonadosomatic index) during the period of reproduction, as well as proportionately larger and heavier gonads, indicating proportionally higher allocation of energy and matter for reproduction.

The condition factor (K) reflects physical and biological state and fluctuations by interaction between feeding conditions, parasitic infections and physiological factors (Le Cren 1951). In this study, the condition factor was always elevated among invertivores, showing that this resource promoved higher well being state if compared to others throphic groups analysed. This also indicates the food reserves shoud have been elevated in all reservoir. So, in some cases, especially in impacted environment, the information on condition factor can be vital to the management because it indicate which organisms are developing (Araneda *et al.,* 2008).

Therefore, there was no significant correlation between this index and the caloric content of the species, although similar trends occurred in some cases. Other studies conducted in the upper Paraná River floodplain also found no correlation between these two variables (Doria & Andrian, 1997). Meanwhile, studies in temperate regions where seasonal variations are more marked have shown the relationship between condition factor and the energy content of fish species (Herbinger & Friars, 1991; Benedito-Cecilio *et al*., 2005). Fluctuations in the energy reserves of structures related to reproduction or feeding that influence the physiology of the organism can be identified through variations in the condition factor (Le Cren, 1951; Soofiani & Hawkins 1982; Encina & Granado-Lorencio, 1997).

Through the quantification of energy balance parameters, one can identify critical periods of energy demand for the animal and study trophic relationships at the population level. One important parameter in this quantification is the caloric values, the values of which, in many cases, have been considered constant and equivalent, regardless of factors such as seasonality and trophic group. Nevertheless, several authors consider the use of fixed values of energy as inappropriate (Prus, 1970; Kitchell *et al*., 1977; Bryan *et al*., 1996) since variations in the caloric values of different trophic groups may affect the calculation of consumption, production, and conversion efficiency. In the present study, significant intra- and interspecific differences in caloric densities were observed, showing that they should be considered when modeling energy flow.

Espínola *et al*. (2012) observed that the condition factor of *Cichla kelberi* was lower in Baía River than in Paraná River, suggesting the influence of the flow regulation by an upstream reservoir (Porto Primavera), with increased transparency due to the retention of fine particles in that reservoir. This process could be facilitating the capture of preys with better nutritional value (Abujanra *et al*., 2009). The process of retention of sediment is more evident in cascade reservoirs, such as Rosana and Segredo, which present transparencies of 2.1 and 1.35 m respectively. Although the Iraí Reservoir has a low transparency (0.95 m) (Júlio Jr *et al*., 2005) compared with other studied reservoirs, the retention of sediment could ease the capture of especially piscivorous and omnivorous species.

Based on the above, we conclude that the species of this study presented a cyclical and similar pattern of energy variation, but this was not reflected in their condition. In addition, an effect of reproduction and feeding habit on the energy allocation was observed for both sexes. Therefore, our results indicate the lack of difference in energy allocation and condition factor between reservoirs, but depending on physical characteristics of the reservoirs (sediment retention), piscivorous and omnivorous species are favored.

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