

Quality and digestibility of food ingested by various trophic fish groups in the Upper Paraná River floodplain

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Abstract: Determining quality of food ingested and digestibility can be helpful in understanding the mechanisms that determine trophic plasticity, which is the ability of a given species to use a more advantageous food source at a given time. In this study, the chemical composition and digestibility of food ingested by various trophic fish groups at different sites of the Upper River Paraná floodplain are evaluated. Specimens of *Pseudoplatystoma corruscans*, *Prochilodus lineatus*, *Leporinus friderici*, *Pterodoras granulosus* and *Schizodon borellii* from the Baía, Ivinheima and Paraná Rivers and from Fechada and Ventura Lagoons were taken as samples (3-16cm-mesh net). Volume participation analyses of food items were determined and contents from the stomach and the intestine's latter quarter were removed for bromatological analysis (energy, crude protein, ash and dry matter). Internal marker acid-insoluble ash was employed for apparent digestibility coefficients. *P. lineatus* and *P. corruscans* had an intake with lower and higher energy and crude protein contents, respectively. *P. corruscans* had slight variations in food items and composition, whereas *P. granulosus* had the greatest variation. Whereas *P. lineatus* had the highest apparent digestibility coefficients in energy, *S. borellii* showed least variation in diet. *P. granulosus* and *P. lineatus* had the higher percentages of dry matter in the stomach in the Paraná River, whereas *P. corruscans* had similar use in the Baía Rivers and Ventura Lagoon. *S. borellii* showed low utilization of germanous energy. It may be concluded that the site determined the variation in quality and use of diet by *L. friderici*, *P. granulosus* and *S. borellii*. The generalist species *L. friderici* demonstrated a good use of different food items ingested at the site; likewise, the generalist species *P. corruscans* had a similar diet and the same use of food. Rev. Biol. Trop. 59 (1): 85-101. Epub 2011 March 01.

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Knowledge of fish diets, which are obtained from the analysis of stomach contents, makes it possible to evaluate the interactive processes within aquatic communities (Winemiller 1989) as well as indicate the composition of ingested items. Such knowledge does not, however, provide information on the assimilation and ratio of the sources of organic nutrients that guarantee the maintenance of these communities as components of the system (Thomas & Cahoon 1993). As such, the caloric value and nutrient levels (Bowen *et al.* 1995) indicate the quality

of ingested food. Additionally, determining digestibility can be helpful in understanding the mechanisms that determine trophic plasticity, which is the ability of a given species to use more advantageous food sources at a given time (Gerking 1994). Trophic plasticity depends on adaptations in the morphology of the digestive system as well as on behavior regarding capture strategies and digestive capacity (Gerking 1994, Abelha *et al.* 2001). Additionally, digestibility provides useful information on the ratios of high or low food utilization levels by fish.

One of the most relevant aspects of the biological efficiency of a food source is its digestibility, which indicates the capacity of animals to digest and absorb the nutrients from a given food component (Hanley 1987), by determining the fraction of nutrient or energy of the ingested food source that is not excreted in feces (NRC 1993). These studies have revealed different availabilities of energy and protein among varied food items for different species and development stages according to food intake habits and the consequent changes in digestion physiology (Bowen *et al.* 1995, Degani *et al.* 1997).

To analyze food intake and its quality, the apparent digestibility coefficients (ADCs) are obtained for energy and macronutrients (protein, carbohydrates, lipids). The availability rates of micronutrients are also important indicators of food quality (Bowen *et al.* 1995, Hemre *et al.* 2003) because they reveal each species' capacity to utilize the food resources available in the environment.

In nutrition studies, the bromatological analysis of an ingested food item is the starting point to determine its quality. This value depends not only on the nutrient content but also on its digestibility. Among the different fish species, there is considerable variation in the ability to digest protein, which is due to the nature and specific activities of each species' proteolytic enzymes (Smith 1978). Nose (1966) reports that, in general, protein is adequately digested by most fish species, except for a few plant protein sources or in the presence of high levels of carbohydrates in the diet. Few studies have been developed in Brazil with this focus in natural environments (Yossa & Araújo-Lima 1998, Silva *et al.* 2000). Some research has shown that the effective assimilation of food by fish depends also on the hydrological regime, environmental condition, water temperature, food intake, and nutrient quantity and quality, as well as the physical state of food items (Silva *et al.* 2000).

The ecological system of the Upper Paraná River floodplain is composed of rivers, channels, and lagoons and has proved to be complex

in regards to the energy flow among its biological compartments and fish species belonging to different trophic groups (Agostinho *et al.* 1997). Studies discussing the digestibility of food resources by the different fish species have not yet been conducted in this system.

In this context, the objective of the present study is to determine the quality and digestibility of the diet ingested by fish belonging to different trophic groups of the Upper Paraná River floodplain, assuming that the following are true: i) individuals of the same species in different environments present various digestibility rates; ii) species with different feeding habits in the same environment present diverse diet utilization; and iii) generalist species satisfactorily use different diets.

MATERIAL AND METHODS

The study sites corresponded to the rivers Baía (RBai), Ivinheima (RiVi), Paraná (Rpar), and the lagoons Fechada (LFec) and Ventura (Lven), all belonging to the Upper Paraná River floodplain ecosystem (22°40' to 22° 50' S; 53° 10 to 53° 40' W (Fig. 1).

Samplings were conducted using gillnets with mesh sizes varying between 3 and 16cm between opposite knots that were set for 24 hours and thereafter checked in 8h intervals (16:00h, 24:00h and 8:00h).

Quarterly field activities were conducted over six days and took place between February 2001 and February 2003, which included the rainy season and a drought period. Five fish species with different feeding habits were selected: *Pseudoplatystoma corruscans* (Agassiz in Spix & Agassiz 1829) (piscivore); *Schizodon borelii* (Boulenger 1900) (herbivore), *Prochilodus lineatus* (Valenciennes 1836) (iliophagous); *Leporinus friderici* (Bloch 1794) and *Pterodoras granulosus* (Valenciennes in Humboldt & Valenciennes 1821) (omnivores).

For diet analysis, 369 adult individuals were studied that belonged to different species and were from the same sampling site and time (Table 1).

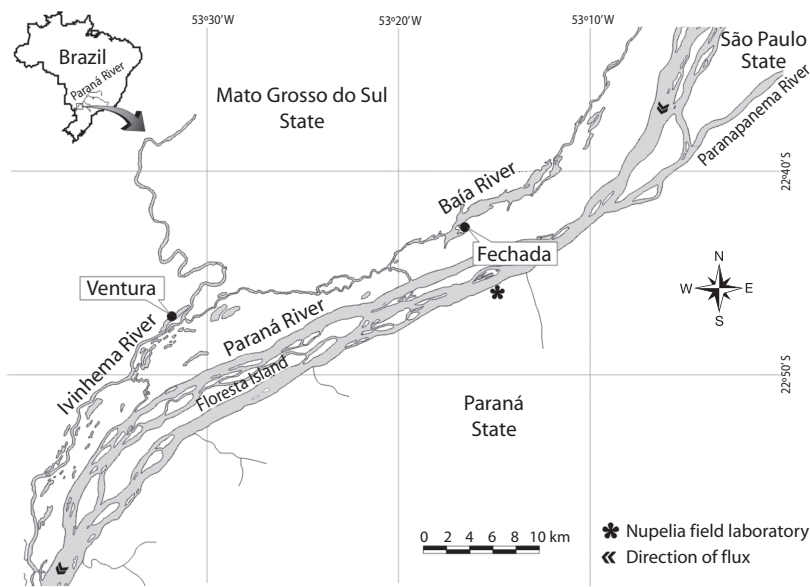


Fig. 1. Study sites corresponded to the rivers Baía (RBai), Ivinheima (Rivi), Paraná (Rpar), and the lagoons Fechada (LFec) and Ventura (Lven), all belonging to the Upper Paraná River floodplain ecosystem.

TABLE 1

Number of individuals used in the stomach analysis by sampling site and mean value and standard deviation of length standard (Ls) and total weight (Wt) of the different species analyzed in the Upper Paraná River floodplain

Fish species	Ls (cm)	Wt (g)	Sampling Site				
			LFec	LVen	RBai	Rivi	RPar
<i>Prochilodus lineatus</i>	36.4±7.2	942.6±178.8	-	16	22	24	23
<i>Leporinus friderici</i>	25.8±2.0	297.3±80.6	-	-	22	32	39
<i>Pterodoras granulosus</i>	50.7±6.3	2 594.6±482.6	-	12	31	25	28
<i>Schizodon borelli</i>	24.2±3.0	320.5±156.7	18	-	-	41	39
<i>Pseudoplatystoma corruscans</i>	76.1±8.1	3 505.8±1 087.7	-	8	7	-	-

LVen=Ventura Lagoon, **LFec**=Fechada Lagoon, **RBai**=Baía River, **Rivi**=Ivinheima River, **RPar**=Paraná River.

Stomach contents were removed, fixed in 4% formalin, and examined under a stereoscopic microscope; items were identified to the lowest possible taxonomic level. This analysis was conducted according to the volumetric method (Hyslop 1980) in which the volume of the items is obtained through displacement of the water column using graduated cylinders. For food items with volumes smaller than 0.1ml, a millimetric plate was used with the

volume expressed in mm³ and later converted to ml (Hellawel & Abel 1971).

From each species, at least five specimens were used from each sampling site. For the analyses of the apparent digestibility coefficient, only the individuals with more than 100mg of material in the stomach and intestine were selected.

After measuring their standard lengths (Ls) and total weights (Wt) (Table 1), the fish

were immediately dissected, and their digestive tracts were extracted. Stomach contents and the contents from the fourth quarter of the intestine were carefully removed so as to avoid mixing mucus with the content. After storage, the samples were kept on ice and later in a freezer (-5°C) until the bromatological composition analysis.

The samples with stomach and intestinal contents were dehydrated in a forced ventilation greenhouse (55°C) for 72h, and later ground (ball mill), refrigerated (-5°C) and analyzed for dry matter, mineral matter (ash), and crude protein according to the methodology described by Silva & Queiroz (2002). To obtain crude energy values, the samples were subjected to combustion in a calorimeter (Parr 1261) at the Energy Ecology Laboratory of the State University of Maringá (UEM), Maringá, Paraná, Brazil.

The apparent digestibility coefficients (ADC) were obtained for dry matter, mineral matter, crude energy, and crude protein through the difference between their ratios and those of the internal marker at the beginning and end of the digestive tract. Acid-insoluble ash was used as the internal marker and quantified according to the methodology proposed by Keulen & Young (1977). To determine the ADCs of dry matter and diet nutrients, the expressions described by Maynard & Loosly (1979) were used.

Apparent digestibility of diet nutrients (DA_N):

$$DA_N = 100 - \left[100 * \left(\frac{\%I_e}{\%I_f} \right) \cdot \left(\frac{\%N_f}{\%N_e} \right) \right]$$

In which DA_N=apparent digestibility of the nutrient; %I_e and %I_f=percentages of indicator in the stomach and at the end of the digestive tract, respectively; %N_e and %N_f=percentages of nutrient in the stomach and at the end of the digestive tract, respectively.

For data analysis, the assumptions of normality (Shapiro-Wilk test) and homocedasticity

(Levene's test) were previously tested to perform the test analyses (MANOVA, ANOVA) using the computer software STATISTICA 6.0. Tukey's t-test was applied whenever significant differences were detected between the means. The significance level assumed for all tests was p<0.05.

RESULTS

Feeding: The volumetric frequency values for the items in the diet of *Prochilodus lineatus*, *Leporinus friderici*, *Pterodoras granulosus*, *Schizodon borellii*, and *Pseudoplatystoma corruscans* in the different subsystems of the Upper Paraná River floodplain are presented in Table 2. The participation of food items in the diet of *P. lineatus* was similar in all subsystems, with a predominance of sediment/detritus.

For *L. friderici*, a variation was observed in the prevalence of the fish, with the greatest volumetric frequency values of the food items ingested in the Baía River (RBai) followed by the Paraná (RPar) and Ivinheima (RIvi) rivers. At RBai, *L. friderici* consumed fewer insects compared with others systems of the Upper Paraná River Floodplain. For *P. granulosus*, there was a more significant consumption of bivalves (*Limnoperma fortunei* and *Corbicula fluminea*) and other mollusks and lower consumption of plants at RPar, as compared to LVen and RIvi. The results of stomach content analysis of *S. borellii* and *P. corruscans* determined there was a predominance of plants and fish, respectively, in all subsystems where these species were sampled. However, *S. borellii* presented differences in ingested items, with the predominance of macrophytes at LFec and RPar and gramineae at RIvi. At RPar, conversely, there was an unusual and noteworthy consumption of fruits and seeds in the stomachs of *S. borellii*.

Chemical composition and diet digestibility:

a) Interspecific comparisons: Caloric content values and crude protein levels in the

TABLE 2
Volumetric frequency values of the food items ingested by Prochilodus lineatus, Leporinus friderici, Pterodoras granulosus, Schizodon borellii and Pseudoplatystoma corruscans in the different food systems of the Upper Paraná River floodplain

Specie Site	<i>P. lineatus</i>			<i>L. friderici</i>			<i>P. granulosus</i>			<i>S. borellii</i>			<i>P. corruscans</i>		
	LVen	RBai	RIvi	RPar	RBai	RIvi	RPar	LVen	RIvi	RPar	LFec	RIvi	RPar	LVen	RBai
<i>Limnoperna fortunei</i>								3.04	4.18	29.20					
<i>Corbicula</i> sp.								2.02	3.20	18.24					
Others mollusks								1.55	2.09	10.0					
Insect					33.10	41.85	36.11								
Insect parts	0.98	0.52	0.44	0.32											
Fish					42.12	26.80	35.48								
<i>Hoplias aff. malabaricus</i>														94.22	83.43
<i>Gymnotus inaequilabiatus</i>														5.78	4.02
<i>Hoplosternun littorale</i>															12.55
Algae	3.55	4.94	5.68	2.36	2.00	3.85	2.36	4.85		2.34			0.52		
Others vegetables					22.58	24.25	25.53	78.95	80.14	20.62					
Aquatic Plants – Macrophyte											99.97		77.91		
Terrestrial Plants – gramineae											99.95				
Fruit/seed								4.38	8.18	4.88					22.03
Sediment/detritus	95.14	94.00	93.78	96.36	0.20	2.40	0.52	2.62	1.09	5.20	0.03	0.05	0.06		
Stone	0.33	0.54	0.54	1.28		0.85		2.58	1.12	8.40					

LVen=Ventura Lagoon, **LFec**=Fechada Lagoon, **RBai**=Baía River, **RIvi**=Ivinheima River, **RPar**=Paraná River.

food items ingested by different species and the digestibility coefficients (ADC) of food items (Fig. 2 and Table 3) (MANOVA, $F_{16, 294}=39.18$, $p<0.01$) showed that the food ingested by *P. lineatus* had lower energy levels (ANOVA, $F_{4, 99}=39.18$, $p<0.01$) than the other species (Tukey, $p<0.001$) and lower protein levels (ANOVA, $F_{4, 99}=90.47$, $p>0.01$) in comparison with *P. corruscans* and *P. granulosis* (Tukey, $p>0.01$). Conversely, *P. corruscans* had the highest levels of energy and protein (Tukey, $p<0.001$). The diet of *L. friderici* had energy values similar to those of *P. granulosis* and *S. borellii*, whereas the protein level was similar only to that of *S. borellii* (Tukey, $p>0.05$) and was lower than that of *P. granulosis* (Tukey, $p<0.001$).

The results of ADC analysis showed *P. lineatus* had better food utilization rates (ANOVA, $F_{4, 99}=37.918$, $p=0.0001$) than *P. corruscans*, *P. granulosis* and *S. borellii* (Tukey, $p=0.0003$; 0.0045 and 0.0011, respectively) and similar rates to *L. friderici* (Tukey, $p>0.05$) (Fig. 2 and Table 4). On the other hand, the protein ADC (ANOVA, $F_{4, 99}=30.047$, $p<0.001$) for this species was higher than those of *L. friderici* and *S. borellii* (Tukey, $p<0.001$) yet similar to *P. granulosis* and *P. corruscans* ($p>0.05$). *Schizodon borellii* had the lowest energy and protein utilization levels (Tukey, $p<0.001$) of all other species. The ADC values of *L. friderici* were similar for energy when compared to *P. granulosis* and *P. corruscans* (Tukey, $p=0.6105$ and 0.0699, respectively); however,

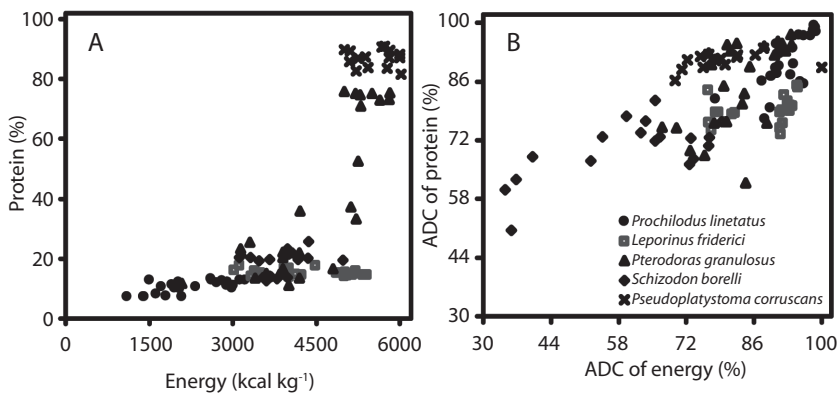


Fig. 2. Protein and energy values (A) of ingested diet and apparent digestibility coefficients (ADC) of crude protein and energy. (B) For five fish species of the Upper Paraná River floodplain.

TABLE 3

Mean energy and protein values in the ingested food items and apparent digestibility coefficients (ADC) of the diet of five fish species of the Upper Paraná River floodplain¹

Specie	Food in stomach		CDA (%)	
	Energy (kcal/kg)	Protein (%)	Energy	Protein
<i>P. lineatus</i>	2253.21±133.28 c	10.61±0.44 c	92.83±1.01 a	90.53±1.33 a
<i>L. friderici</i>	4266.30±171.32 b	15.43±0.25 c	87.48±1.57 ab	79.07±0.70 b
<i>P. granulosis</i>	4360.14±193.32 b	37.51±4.98 b	83.82±1.46 b	86.19±1.98 a
<i>S. borellii</i>	3885.95±103.96 b	18.55±0.92 c	60.54±3.54 c	70.08±1.70 c
<i>P. corruscans</i>	5554.21±92.55 a	86.97±0.76 a	79.59±1.98 b	90.93±0.49 a

¹Values in the same column followed by the same letter do not differ significantly by Tukey's test ($p>0.05$).

TABLE 4
 Mean values for bromatological composition of stomach and intestine contents of five fish species
 from the Upper Paraná River floodplain¹

Local	Energy (kcal/kg)		Protein (%)		Ash (%)		Dry matter (%)	
	Stomach	Intestine	Stomach	Intestine	Stomach	Intestine	Stomach	Intestine
<i>Prochilodus lineatus</i>								
LVen	2851.52 ±240.45 a	1044.68 ±221.21 a	11.27 ±0.52 a	4.89 ±0.32 a	43.86 ±1.66 a	70.23 ±7.27 a	88.92 ±1.47 a	89.13 ±3.69 ab
RBai	1932.58 ±117.33 b	458.01 ±52.16 b	10.71 ±0.47 a	4.30 ±0.44 a	46.83 ±0.84 a	74.09 ±5.43 a	89.51 ±1.48 a	91.86 ±1.27 a
RIvi	2758.55 ±52.44 a	869.37 28.21 a	11.91 ±0.33 a	4.47 ±0.88 a	47.81 ±1.66 a	67.33 ±2.82 a	93.11 ±1.32 a	83.43 ±4.07 ab
RPar	1569.91 ±140.98 b	116.62 ±24.75 b	7.25 ±0.14 b	0.56 ±0.11 b	45.01 ±3.47 a	69.61 ±2.90 a	93.37 ±1.41 a	78.60 ±1.57 b
<i>Leporinus friderici</i>								
RBai	3687.14 ±177.82 b	808.01 ±19.92 b	15.67 ±0.51 a	10.21 ±0.15 a	38.06 ±1.98 a	60.09 ±5.21 a	88.87 ±1.12 a	89.03 ±2.52 a
RIvi	3946.17 ±224.61 b	1541.22 ±536.14 b	14.66 ±0.28 ab	10.41 ±0.22 a	39.00 ±3.25 a	58.73 ±5.51 a	90.17 ±1.12 a	90.67 a ±1.64
RPar	5165.58 ±60.71 a	3464.22 ±134.11 a	14.35 ±0.25 b	10.43 ±0.17 a	18.89 ±2.29 b	46.50 ±4.70 a	88.32 ±2.02 a	89.69 ±1.83 a
<i>Pterodoras granulosus</i>								
LVen	4033.03 ±383.30 b	2802.15 ±310.16 a	27.69 ±3.98 b	10.10 ±2.11 a	7.45 ±0.64 b	23.02 ±2.58 b	93.35 a ±1.13 a	90.97 ±2.39 b
RIvi	3785.91 ±122.13 b	3033.43 ±234.90 a	15.55 ±1.23 c	14.00 ±1.04 a	6.12 ±0.32 b	14.77 ±1.75 b	94.03 ±1.02 a	93.08 ±1.27 b
RPar	5445.94 ±105.43 a	1420.32 ±82.31 b	71.62 ±0.56 a	12.38 ±0.53 a	22.40 ±1.21 a	56.98 ±4.27 a	91.95 ±1.50 a	76.73 ±1.82 a
<i>Schizodon borellii</i>								
LFec	4177.63 ±67.14 a	3379.42 ±192.94 a	21.09 ±0.91 a	11.29 ±0.25 a	18.36 ±4.93 a	58.44 ±8.86 a	91.63 ±0.96 a	90.33 ±2.55 a
RIvi	3769.76 ±275.23 a	3410.09 ±364.65 a	19.49 ±0.39 a	10.90 ±0.17 a	16.20 ±1.39 a	45.16 ±4.04 a	91.28 ±1.01 a	88.53 ±2.29 a
RPar	3710.47 ±64.05 a	1180.24 ±35.86 b	13.15 ±0.23 b	4.90 ±0.10 b	13.30 ±1.37 a	44.78 ±5.00 a	86.37 ±1.34 b	88.98 ±2.03 a
<i>Pseudoplatystoma corruscans</i>								
LVen	5538.08 ±143.21 a	3746.29 ±151.22 a	84.69 ±0.96 a	26.35 ±0.87 a	46.57 ±1.58 a	64.58 ±4.17 a	87.38 ±1.70 a	86.59 ±2.25 a
RBai	5568.33 ±129.13 a	3824.14 ±257.48 a	82.88 ±1.22 a	21.71 ±1.12 b	48.13 ±1.50 a	65.69 ±3.48 a	89.47 ±1.56 a	82.47 ±3.83 a

LVen=Ventura Lagoon, LFec=Fecheda Lagoon, RBai=Baía River, RIvi=Ivinheima River, RPar=Paraná River.

¹Values regarding the same fish in the same column followed by the same letter do not differ significantly by the Tukey test (p>0.05) or ANOVA (p>0.05).

the protein ADCs for *L. friderici* were lower than those of *P. granulosis* (Tukey, $p < 0.05$) and *P. corruscans* (Tukey, $p < 0.001$). *Pterodoras granulosis* and *P. corruscans* had similar energy utilization (Tukey, $p > 0.05$) and protein levels (Tukey, $p > 0.05$).

b) Spatial comparisons: The study observed an effect of the site on the chemical composition (energy, crude protein, mineral matter, and dry matter) and digestibility coefficients (ADC) of the diet for *P. lineatus* (MANOVA, $F_{36, 24, 365} = 5.1558$, $p = 0.0004$), *P. granulosis*, (MANOVA, $F_{24, 26} = 17.335$, $p = 0.0001$), *L. friderici* (MANOVA, $F_{24, 14} = 5.100$, $p = 0.001$), and *S. borellii* (MANOVA, $F_{24, 8} = 39.164$, $p = 0.00001$). For *P. corruscans*, however, an effect was observed only for protein content in the intestine (MANOVA, $F_{12, 2} = 0.87095$, $p = 0.65027$).

Prochilodus lineatus: The energy content of food in the stomach (ANOVA, $F_{3, 19} = 18.989$, $p = 0.00001$) and intestine of this species (ANOVA, $F_{3, 19} = 16.927$, $p = 0.00001$) was higher for specimens sampled at LVen in comparison with those from RBai (Tukey, $p < 0.001$) and RPar (Tukey, $p < 0.05$). However, these levels did not differ from those observed for Rivi (Tukey, $p > 0.0001$) (Table 4).

The percentages of crude protein in the stomach (ANOVA, $F_{3, 19} = 30.779$, $p = 0.000001$) and intestine (ANOVA, $F_{3, 19} = 14.207$, $p = 0.00004$) were greater at Rivi than at RPar (Tukey, $p = 0.00181$ and $p = 0.0004$, respectively). These values, however, did not differ from the values observed at LVen (Tukey, $p = 0.656264$ and $p = 0.9502$, respectively) and RBai (Tukey, $p = 0.136501$ and $p = 0.9950$, respectively). The levels of crude protein at LVen in the stomach (Tukey, $p = 0.00182$) and intestine (Tukey, $p = 0.0003$) and at RBai in the stomach (Tukey, $p = 0.0019$) and intestine (Tukey, $p = 0.0006$) were also greater than those obtained at RPar but did not differ among themselves (Tukey, $p = 0.741662$ and $p = 0.870485$, respectively).

There was no difference between the values for mineral matter in the stomachs (ANOVA,

$F_{3, 19} = 0.64019$, $p = 0.59847$) and intestines (ANOVA, $F_{3, 19} = 0.37043$, $p = 0.77522$) as well as in dry matter in the stomachs of the individuals sampled at the different sites. However, a greater level of dry matter was observed in the intestine at RBai (ANOVA, $F_{3, 19} = 4.4096$, $p < 0.05$) compared to at RPar (Tukey, $p < 0.05$), although no differences were observed among the other averages (Table 4).

Leporinus friderici: For this species, the energy contents of the stomach (ANOVA, $F_{2, 18} = 0.0001$) and intestine (ANOVA, $F_{2, 18} = 18.459$, $p = 0.0004$) were higher at RPar (Tukey, $p < 0.001$) when compared to RBai. The mean obtained at RPar for both the stomach (Tukey, $p < 0.001$) and the intestine (Tukey, $p = 0.00142$) was higher than at Rivi (Tukey, $p < 0.001$). No differences were observed between RBai and Rivi values in either portion of the digestive tract (Tukey, $p = 0.053624$ and $p = 0.0261651$, respectively) (Table 4).

The level of crude protein in the stomach (ANOVA, $F_{2, 18} = 3.5951$, $p = 0.04857$) was higher at RBai in comparison to RPar (Tukey, $p = 0.0490$). The values at both RBai (Tukey, $p = 0.150367$) and RPar (Tukey, $p = 0.821744$) did not differ from those for Rivi with no significant differences in the intestine (ANOVA, $F_{2, 18} = 0.45712$, $p = 0.64026$) among crude protein levels for this species, regardless of sampling site.

Pterodoras granulosis: The energy value of stomach contents (ANOVA, $F_{2, 24} = 13.099$; $p < 0.01$) was higher at RPar in relation to Rivi (Tukey, $p < 0.001$); in the intestine, (ANOVA, $F_{2, 24} = 12.693$, $p = 0.00017$) the energy value was higher at Rivi than at RPar (Tukey, $p < 0.001$) (Table 4).

The level of crude protein in the stomach (ANOVA, $F_{2, 24} = 138.73$, $p < 0.01$) was different in all environments (Tukey, $p < 0.01$); however, no differences were observed among the values of these nutrients (ANOVA, $F_{2, 24} = 2.0149$, $p = 0.15527$) in the intestines of fish from the different sites.

The levels of ash in the stomach (ANOVA, $F_{2, 24}=137.44$, $p=0.000001$) and the intestine (ANOVA, $F_{2, 24}=57.957$, $p=0.000001$) of fish from RPar were higher than those from Rivi (Tukey, $p<0.001$). At Lven, the obtained values did not differ from the stomach (Tukey, $p>0.05$) and intestine (Tukey, $p>0.05$) values for fish from Rivi and Rpar. These were, however, different values from those obtained at RPar for the stomach (Tukey, $p<0.001$) and intestine (Tukey, $p<0.001$).

There was no effect of the subsystems on the means obtained for dry matter in the stomach (ANOVA, $F_{2, 24}=075.915$, $p=0.47898$). However, intestinal levels of individuals from LVen and Rivi did not differ (Tukey, $p>0.05$) but were higher than those observed for RPar (Tukey, $p<0.001$).

***Schizodon borellii*:** The results of the ANOVA obtained for *S. borellii* indicated that there were no differences in the stomach energy contents ($F_{2, 15}=2.3003$, $p=0.13449$), ash in the stomach ($F_{2, 15}=0.68770$, $p=0.5179$), ash in the intestine ($F_{2, 15}=1.5158$, $p=0.25144$), and dry matter in the intestine ($F_{2, 15}=0.16542$, $p=0.84906$) as a result of the subsystems. However, differences were found in the intestine energy contents ($F_{2, 15}=28.6020$, $p=0.00001$) with higher values at RPar than at LFec (Tukey, $p<0.001$) and Rivi (Tukey, $p<0.001$); however, the latter two sites had similar means (Tukey, $p=0.9956$) (Table 4).

In regards to the levels of crude protein in the stomach (ANOVA, $F_{2, 15}=51.678$, $p=0.0001$) and intestine (ANOVA, $F_{2, 15}=375.44$, $p=0.000001$), observed mean values were lower at RPar in relation to LFec (Tukey, $p<0.001$) and Rivi (Tukey, $p<0.001$); however, there was no difference between values in the stomach (Tukey, $p=0.163479$) and intestine (Tukey, $p=0.3293$) at LFec and Rivi.

For dry matter level in the stomach, differences were observed (ANOVA, $F_{2, 15}=6.9641$, $p=0.00726$) with lower values at RPar than at LFec (Tukey, $p<0.05$) and Rivi (Tukey, $p<0.05$) (Table 4).

There was an effect of the subsystems for ash values in the stomach (ANOVA, $F_{2, 18}=19.585$, $p=0.00003$) with similar mean values for Rivi and RBai (Tukey, $p=0.964032$), which were higher than at RPar (Tukey, $p<0.001$). There were no differences in ash values in the intestine (ANOVA, $F_{2, 18}=2.1134$, $p=0.14982$) or in dry matter percentages in the stomach (ANOVA, $F_{3, 19}=4.4096$, $p=0.01628$) and intestine (ANOVA, $F_{2, 18}=0.16413$, $p=0.84988$).

***Pseudoplatystoma corruscans*:** No differences were observed in the mean values of subsystems LVen and RBai for energy contents in the stomach ($F_{1, 13}=0.2473$, $p=0.8775$) and intestine ($F=0.6295$, $p=0.80582$), protein levels in the stomach ($F=1.3081$, $p=0.27336$), ash in the stomach ($F=0.51517$, $p=0.48561$) and intestine ($F=0.04274$, $p=0.83941$), and dry matter in the stomach ($F=0.82332$, $p=0.38072$) and intestine ($F=0.79658$, $p=0.38839$). However, protein levels in the intestine at LVen were higher ($F=10.258$, $p=0.00693$) than those at RBai (Table 4).

Diet digestibility: Energy (Fig. 3A): In regards to the Apparent Digestibility Coefficients (ADC) of energy (ANOVA, $F_{3, 19}=8.6852$, $p<0.01$) (Fig. 3A) for *P. lineatus*, the values obtained at RPar were higher than at Rivi (Tukey, $p=0.0114$) and LVen (Tukey, $p=0.006$) but did not differ from those observed for RBai (Tukey, $p=0.0903$). The ADC for this species at LVen did not differ from those found at Rivi (Tukey, $p=0.4210$) and RBai (Tukey, $p=0.0881$). No differences were observed (Tukey, $p=0.7482$) between the values for RBai and Rivi.

For *P. granulosus*, the energy ADC at RPar (ANOVA, $F_{2, 24}=15.413$, $p<0.01$) was higher than at LVen (Tukey, $p<0.01$) and Rivi (Tukey, $p<0.01$). However, there was no difference between the values at LVen and Rivi (Tukey, $p=0.277615$). For *L. friderici* (ANOVA, $F_{2, 18}=32.405$, $p<0.01$), a lower ADC value was observed at RPar than at RBai and Rivi (Tukey, $p<0.01$), but the values for RBai and Rivi were similar to one another (Tukey, $p=0.173612$).

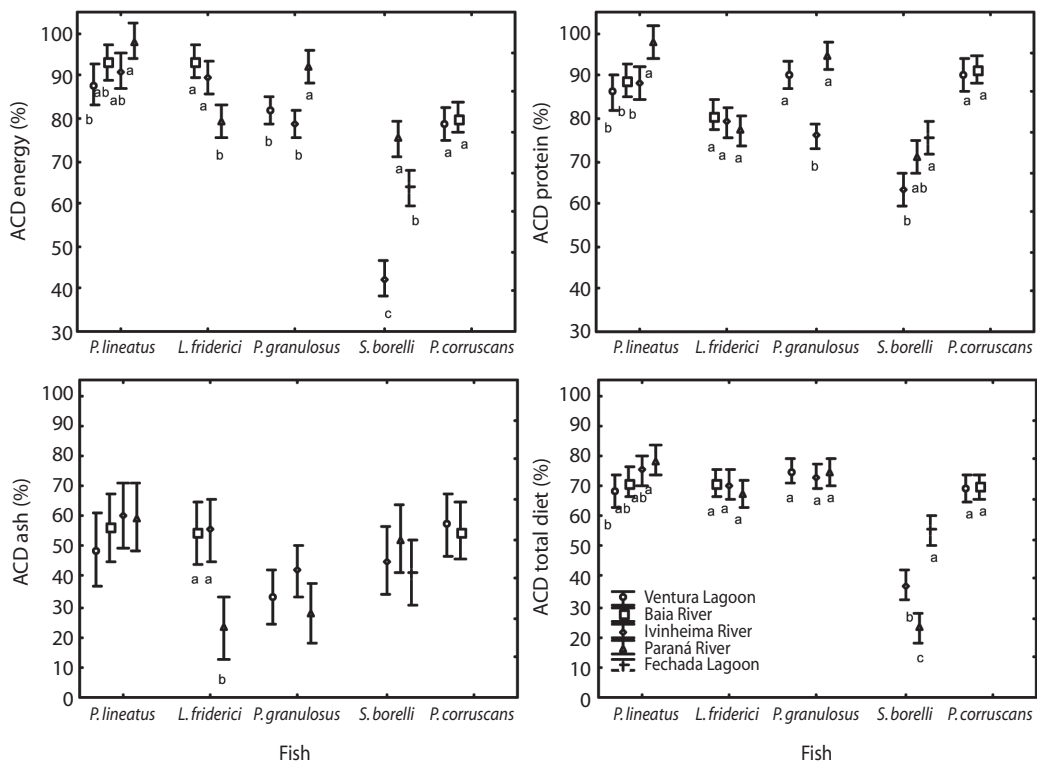


Fig. 3. Means and standard deviation (bars) of the apparent digestibility coefficients (ADC) of energy, crude protein, mineral matter, and total food consumed by five species in different subsystems of the Upper Paran River floodplain¹.

¹Values regarding the same fish in the same column followed by the same letter do not differ significantly by the Tukey test ($p > 0.05$) or ANOVA ($p > 0.05$).

The energy ADCs of the diet of *S. borellii* (ANOVA, $F_{2, 15} = 55.040$, $p < 0.01$) were different in all subsystems with higher values at RPar than at LFec (Tukey, $p < 0.01$) and RIVI (Tukey, $p < 0.01$), whereas the values observed at RIVI were lower (Tukey, $p < 0.01$) than those for LFec. For *P. corruscans*, the energy ADCs at RBai and LVen were similar (ANOVA, $F_{12, 2} = 0.87095$, $p = 0.65027$).

Protein (Fig. 3B): The crude energy ADC for *P. lineatus* (ANOVA, $F_{3, 19} = 7.2201$, $p = 0.00199$) was higher at RPar than at LVen (Tukey, $p < 0.01$), RBai (Tukey, $p < 0.05$) and RIVI (Tukey, $p < 0.05$). However, the values at RBai were similar to those at LVen (Tukey, $p = 0.756804$) and RIVI (Tukey, $p = 0.9973$). The

latter two subsystems featured values that did not differ from one another (Tukey, $p = 0.8597$).

For *L. friderici*, there was no difference in the crude protein ADCs (ANOVA, $F_{2, 18} = 3.2318$, $p = 0.06321$) in the subsystems. For *P. granulosus* (ANOVA, $F_{2, 24} = 18.823$, $p < 0.01$), RPar and LVen had similar values (Tukey, $p = 0.365568$), which were higher than those observed at RIVI (Tukey, $p < 0.01$). The digestibility of this nutrient for *S. borellii* (ANOVA, $F_{2, 15} = 7.7988$, $p < 0.01$) was greater at LFec than at RIVI (Tukey, $p < 0.01$); however, both environments had values that did not differ from those obtained at RPar (Tukey, $p = 0.313759$ and $p = 0.071818$, respectively). The protein ADCs at LVen and RBai for *P. cor-*

ruscans (ANOVA, $F_{1,13}=0.24448$, $p=0.62924$) were statistically similar.

Ash (mineral matter) (Fig. 3C): The ANOVA of the mineral matter ADC for *P. lineatus* ($F_{3,19}=1.0578$; $p=0.3902$), *P. granulatus* ($F_{2,24}=1.1296$, $p=0.33975$), *S. borellii* ($F_{2,15}=2.015$, $p=0.16785$), and *P. corruscans* ($F_{1,13}=0.23525$, $p=0.63573$) were not affected by the different sites. However, for *L. friderici* (ANOVA, $F_{2,18}=29.086$, $p=0.0001$), a lower ADC was observed at RPar than at RBai and RIVI (Tukey, $p<0.001$), whereas the values for RBai and RIVI did not differ from one another (Tukey, $p=0.9730$).

Total diet (Fig. 3D): No effects of the subsystems were observed on the total diet ADCs for *L. friderici* (ANOVA, $F_{2,18}=1.5897$, $p=0.23132$) and for *P. granulatus* (ANOVA, $F_{2,24}=0.25180$, $p=0.77943$). For *P. lineatus* individuals (ANOVA, $F_{3,19}=4.4653$, $p=0.01554$), the total diet digestibility at RPar did not differ from RBai (Tukey, $p=0.01097$) and RIVI (Tukey, $p=0.7079$) but was higher than that at LVen (Tukey, $p=0.0145$). The values for LVen did not differ from those for RBai (Tukey, $p=0.6878$) and RIVI (Tukey, $p=0.1154$). The total diet digestibility at RBai was similar to that for RIVI (Tukey, $p=0.5554$).

The total diet ADC for *S. borellii* (ANOVA, $F_{2,15}=17.501$, $p>0.001$) at LFec was higher than at RIVI and RPar (Tukey, $p=0.0116$ and $p<0.001$, respectively). However, the values at RIVI and RPar did not differ from one another (Tukey, $p>0.05$). No differences were found between the total diet digestibility at RPar and LVen (ANOVA, $F_{1,13}=0.02424$, $p=0.87866$) for *P. corruscans* individuals.

DISCUSSION

***Prochilodus lineatus*:** In spite of having the ingested food with the lowest energy and protein contents, *P. lineatus* had elevated Apparent Digestibility Coefficients (ADC) for both measurements, which indicates that this species possesses a digestive system that is

able to efficiently use a nutritionally poor food source (Bowen *et al.* 1995). Another strategy that allows such efficiency is the ability to ingest large quantities of food in relation to body weight (Yossa & Araújo-Lima 1998). The fact that there were discrepancies in energy, protein, and ADC contents for *P. lineatus* may be related to the quantity of ingested food because the diet of *P. lineatus* is mainly composed of detritus and sediment (Table 1) (Hahn *et al.* 2002). Although the energy levels at Rpar were higher than at LVen and RIVI, the higher total diet ADCs of both at the site indicates that the diet was composed of more digestible items for that species.

The food energy values at Rpar and values of crude protein (7.25 to 11.27%) in the food consumed by *P. lineatus* in this study are similar to those found by Bowen *et al.* (1984), with 7.3 to 18.3% in the detritus ingested by *Prochilodus platensis* in the Mid Paraná, Río de la Plata, Argentina, and slightly higher than that found for *P. nigricans* by Yossa & Araújo-Lima (1998).

Total diet and protein ADCs found for *P. lineatus* in this study for all environments are higher than those reported by Yossa & Araújo-Lima (1998) for *Prochilodus nigricans* and *Liposarcus pardalis* in lagoons of the Central Amazon floodplain and by Bowen (1981) for *Tilapia mossambica* consuming periphyton attached to the detritus. Yossa (2002) reported low food digestibility of Curimatidae and Prochilodontidae from the Amazon basin, which indicates that the food items consumed by *Prochilodus* in the Paraná River basin are more digestible.

Although *P. lineatus* had similar intake habits in the different subsystems, the levels of energy, protein, and ash in the stomach varied according to site, especially for the data from Rpar and LVen. These differences are probably due to the variations in organism participation in the decomposition chain, such as algae, bacteria and fungi, which were not observed in the stomach content analysis due to the high level of decomposition.

The high level of ash (43 to 47%) observed in the food ingested by *P. lineatus* is in accordance with reports for other detritivorous species, which have diets comprised of between 10 and 70% organic matter (Bowen 1984, Araújo-Lima & Hardy 1987). However, Yossa & Araújo-Lima (1998) observed lower values for *P. nigricans* than those values for *P. lineatus* in this study. This elevated participation of mineral matter in the food ingested by *P. lineatus* is justified by the strategy of food collection by detritivorous fish species.

***Leporinus friderici*:** Although differences were identified for protein levels and consumed items in the different subsystems, protein ADCs did not differ, which indicates that this species equally utilizes protein from different sources, such as fish and insects, which demonstrates its omnivorous eating habits (Hahn *et al.* 1997, Hahn *et al.* 1998; Balassa *et al.* 2004) and opportunist behaviors (Balassa *et al.* 2004). The higher energy value and lower energy ADC at RPar reflects a difference in the chemical composition of the ingested food item, which is reinforced by the lower level of mineral matter in the diet of fish from RPar. Thus, even though this fish presented the same feeding habit in the different environments, there was an intake of higher energy items (animal or plant) at RPar. The protein levels verified for the diet ingested by *L. friderici* were slightly below those observed for *Colossoma macropomum* during the flood period (11 to 15%) by Silva *et al.* (2000) when fruits and plants are the basis of this species' diet.

The satisfactory utilization of food by *L. friderici* with varying chemical compositions among the subsystems may enable feeding plasticity, which occurs in this species and a few others in the floodplain due to the ecosystem diversity and the hydrologic regime, which cause seasonal variation in food availability (Hahn *et al.* 2002, Marçal-Simabuku & Peret, 2002). Cyrino (1984) and Oliveira-Filho & Fracalossi (2006) also did not observe differences in the utilization of animal or vegetal protein for *Brycon cephalus* and *Rhamdia*

quelen, respectively, both of which are omnivores. However, Borghetti *et al.* (1991) report that *Piaractus mesopotamicus* requires part of its diet (23%) to be of animal origin, although it features high ADCs for energy and protein for food from animal and plant sources (Abimorad & Carneiro 2004), whereas Meer *et al.* (1995) and Faria *et al.* (2001) highlight that *Colossoma macropomum* and *Leporinus macrocephalus*, respectively, utilize vegetal protein more favorably than other species.

***Pterodoras granulosus*:** The food items consumed by *P. granulosus* had the highest variation in composition, in terms of ingested items, caloric values, and levels of protein and ash in the subsystems. The higher levels of protein and ash found at RPar are due to the greater participation of bivalves in the food ingested in that environment. This greater capacity to utilize food energy and protein at RPar indicates that this fish, although it displays great diet plasticity, also better utilizes animal prey, such as bivalves. This result supports studies by Silva *et al.* (2005). These authors affirm that *P. granulosus* is able to utilize soft tissues from both *C. fluminea* and *L. fortunei* without damaging their shells. The possibility that *C. fluminea* represents up to 90% of the diet was reported by Gaspar da Luz *et al.* (2002). As such, although this species is considered omnivorous in the Upper Paraná River floodplain (Hahn *et al.* 1992, Hahn *et al.* 1998; Gaspar da Luz *et al.* 2002) with a diet that reflects the abundance of feeding resources in the different environments of that plain (Cantanhêde *et al.* 2006) with a strong tendency towards herbivory (Hahn *et al.* 1992), the results indicate the species makes better use of an animal-based diet in the absence of plant-based sources. This was also demonstrated through stable isotope analysis, given its trophic position, which occupied the third trophic level (Faria 2007).

A variation in the composition of the ingested diet, similar to that observed in this work for *P. granulosus*, was reported by Silva *et al.* (2000) for *Colossoma macropomum*. They noted that this species' energy and

protein levels markedly increased from season to season due to zooplankton intake, varying between 11% and 57% of protein and 484.6 to 574.2kcal/g in the drought and flood seasons, respectively.

The better utilization of animal-based protein by *P. granulosus* differed from that observed by Meer *et al.* (1995) for *C. macropomum*, which are species considered to be omnivorous with a strong herbivore tendency. These authors affirmed that individuals from this species make better use of plant-based protein.

During dissection of the final portion of the digestive tract of *P. granulosus*, it was observed that *C. fluminea* shells were intact (without their inner content). This low digestibility of the shell is due to the fact it is composed basically of calcium, a nutrient that is required in low quantities for fish (approximately 1%, NRC 1993) and is therefore poorly absorbed in high levels, as in the diet of *P. granulosus* at Rpar.

The fact that *P. granulosus* has better digestibility of animal-based food items may be related to the enzymatic activity of this species and the composition of vegetal tissues. According to Gerking (1994), the digestion level of food items varies according to their origin, and vegetal-based sources are less digested than animal-based items for most fish. This is because the cellular wall hinders the penetration and action of digestive enzymes. Thus, compounds such as cellulose and lignin reduce the digestibility of ingested food items.

***Schizodon borellii*:** The variation in the participation of ingested items at the different sites, as indicated by the stomach content analysis of *S. borellii*, was confirmed by the results of the bromatological composition. Thus, at the sites where more plants (macrophytes or gramineae) were consumed, the levels of protein were similar.

The different energy ADCs for *S. borellii* in the different environments was influenced by a better utilization of food items containing macrophytes and fruits. At RPar, this is due

to the fact that fruit and seed tissues are more digestible than structural tissue (Bowen *et al.* 1995); some Brazilian fish species have better utilization of seeds and grains than of fish meal (Faria *et al.* 2001, Silva *et al.* 2003). It is important to emphasize that the energy and protein digestibility of gramineae (RiVi) was lower than that of macrophytes (LFec), which indicates higher availability of these nutrients in macrophytes. Even so, *S. borellii* is a strictly herbivorous species (Hahn *et al.* 2002) and it had variations in diet utilization; this difference is due to fact that Gramineae have more support tissue, which results in lower energy content (Bowen *et al.* 1995). The caloric content utilization of Gramineae (RiVi) by *S. borellii* was similar to that obtained by Buddington (1979) for *Najas guadalupensis* ingested by *Tilapia zilli* (45.4%), whereas macrophytes (LFec) presented higher energy digestibility.

Total diet ADCs, which recorded only plants (RiVi and LFec), were lower than those found for cichlid *Eetroplus suratensis* fed with *Hydrilla verticellata* (50-51.9%) by De Silva & Perera (1983), *Tilapia nilotica* fed with Cyanophyta (43%) by Moriarty & Moriarty (1973) and *Stegaster nigricans* fed with *Enteromorpha* algae (75%) by Galetto & Bellwood (1994). On the other hand, they were higher than those values reported by Buddington (1979) for *T. zilli* feeding on *Najas guadalupensis* (29.3%). Protein digestibility at RiVi (Gramineae) was similar to that obtained by De Silva & Perera (1983) feeding *H. verticellata* to *E. suratensis* (65.6%). However, at LVen (macrophytes), protein utilization by *S. borellii* was higher than those reported in this study.

Protein digestibility of macrophytes (LFec) in this study was similar to that found in *Najas guadalupensis* for *T. zilli* (75.1%) by Buddington (1979) and for the algae *Enteromorpha* for *S. nigricans* by Galetto & Bellwood (1994).

***Pseudoplatystoma corruscans*:** *Pseudoplatystoma corruscans* ingested mainly fish, which resulted in a small variation in ingested items, with individuals at RBai featuring a small reduction in the participation of *Hoplias*

malabaricus and the occurrence of *Hoplosternum littorale*. At RBai, there were no oscillations in food quality (bromatological composition) or in digestibility, and ADCs remained high (about 70% of ACD total diet). This is due to the fact that *P. corruscans* is a specialist species and therefore has few diet alterations (Bowen 1983, Gerking 1994, Hahn *et al.* 2002).

With the objective of determining the digestibility coefficient for *P. corruscans* in an experimental essay, Gonçalves & Carneiro (2003) found values of 84.1% for protein and 72.8% for energy when fish were fed with fish meal and lower values when fed with plant-based protein-rich items. In the present study, the energy and protein ADC values for *P. corruscans* are higher than those reported by the aforementioned authors. These differences are possibly due to the fact that fish meal contains residue from processing (Faria *et al.* 2001) and therefore has higher levels of ash, which reduces food digestibility.

The present study made it possible to verify the existence of a wide range in the composition of ingested food items, especially in regards to energy contents and protein levels by the different species. In some cases, as in that for *P. granulosus*, variations were found in the diet ingested by the same species at different sites. In general, these variations agree with those described by Bowen *et al.* (1995). Thus, the lowest caloric values and crude protein levels occurred in the food items ingested by the detritivorous species (*P. lineatus*), followed by the herbivores (*S. borellii*) and omnivorous species (*L. friderici* and *P. granulosus*), with the highest energy and protein values obtained in the diet of *P. corruscans* (piscivore).

The occurrence of ash absorption by all species analyzed in this study and also reported by Bowen (1981) for *T. mossambica*, as well as the difference in their ADCs for *L. friderici*, contributes to the hypothesis that, although it is used as an indicator in several fish studies (Getachew 1988), ash may not represent the best indicator for digestibility studies in natural environments for the species in this report. In

this study, acid-insoluble ash was used as the internal marker, which according to Buddington (1980), Bowen (1981) Galetto & Bellwood (1994), Yossa & Araújo-Lima (1998) and Vidal *et al.* (2004), constitutes a good indicator in fish digestibility studies because it is not affected by the digestion process and is not assimilated.

Deforestation, overfishing, stocking of exotic species, pollution, and construction of dams have changed, and overfishing has drastically changed, the main ecosystems, both in relation to stocks and biodiversity (Barbarino-Duque *et al.* 1998). The Paraná River Basin, the second largest in South America, suffers from the many dams that constrict the movement of stocks of the commercial fish species examined in this study (Okada *et al.* 2005). The only free stretch of the basin, the floodplain of the Paraná River, has guaranteed suitable ecological conditions for breeding, feeding, and growth to sustain the stocks exploited in the downstream, the Itaipu Reservoir, where the community depends on the riverside commercial fishing, (artisanal, and subsistence fisheries). Therefore, it is important to remove the old practices (pollution, stocking) and maintain the forest on the banks of major rivers that form the basin. The present study provides evidence for conservation of the natural environment, and further investigations are needed to understand the influence of seasons and physiological characteristics of the species (sex and maturity stage) so that fish managers can better inform themselves for the drafting of legislation that will be more appropriate both for fishing and for the protection of biodiversity. Determining food digestibility in a natural environment may provide guidelines for conservation and management practice of commercially important fish stocks in the Upper Paraná River floodplain, in addition to providing valuable information on ecological aspects of the different fish species. This knowledge could also be used in aquaculture to determine feeding management and the formulation of rations.

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RESUMEN

Determining quality of food ingested and digestibility can be helpful in understanding the mechanisms that determine trophic plasticity, which is the ability of a given species to use a more advantageous food source at a given time). El objetivo de este estudio fue evaluar la composición química y la digestibilidad de los alimentos consumidos por los peces de los diferentes grupos tróficos en diferentes lugares de la llanura de inundación del alto río Paraná. Fueron colectados (red 3 a 16cm de tela) individuos de *Pseudoplatystoma corruscans*, *Prochilodus lineatus*, *Leporinus friderici*, *Pterodoras granulosus* y *Schizodon borellii* en los ríos Baía (Rbai) Ivinheima (Rivi) y Paraná (RPar), lagunas Fechado (LFec) y Ventura (LVen). Se realizaron análisis de la participación en volumen de elementos alimentarios como contenido estomacal y el contenido de la cuarta parte final del intestino fue removido para análisis bromatológicos (energía, proteína, cenizas y materia seca). Se determinaron los coeficientes de digestibilidad aparente (CDA) utilizando las cenizas insolubles en ácido como marcador interno. *P. lineatus* y *P. corruscans* consumieron alimentos con menores y mayores contenidos de energía y proteína bruta, respectivamente con *P. corruscans* teniendo poca variación en los elementos y en la composición del alimento, mientras que PG presentó la mayor variación de estos. *P. lineatus* tuvo mejores CDA de la energía y *S. borellii* presentó la menor utilización de energía alimentaria. *P. granulosus* y *P. lineatus* tuvieron un mejor uso del alimento en el RPar y *P. corruscans* presentó aprovechamiento similar en el RBai y LVen. *Schizodon borellii* tuvo bajo aprovechamiento de la energía proveniente de las gramíneas. Se concluye que *L. friderici*, *P. granulosus* e *S. borellii* presentaron variación en la calidad y en el aprovechamiento del alimento consumido debido a los subsistemas. El *L. friderici*, especie generalista, presen-

tó buena utilización de los diferentes alimentos consumidos en los subsistemas, mientras que *P. corruscans*, especialista, tenía una dieta similar y el mismo aprovechamiento.

Palabras clave: peces, dieta, energía, nutrición, niveles tróficos, Río Paraná.

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