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Research Article

Factors structuring the fish community in the area of the Coaracy Nunes hydroelectric reservoir in Amapá, northern Brazil

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Abstract

The objective of this study was to document the structure of the fish assemblages found in the aquatic environments affected by the Coaracy Nunes hydroelectric reservoir in Ferreira-Gomes, Amapá (Brazil) and the principal factors that determine this structure. In order to do this, standardized samples were collected of the fauna and the environmental parameters in the four principal sectors of the reservoir (upstream, the reservoir, the lake, and downstream). Fish species richness, abundance, and biomass were estimated for each sector. The abundance data were analyzed using null models of co-occurrence. A multivariate BIO-ENV analysis was used to examine the relationship between biological and environmental factors. The relationship between species richness and biomass of both prey and predator species was analyzed to determine whether predation was affecting community structure. Size spectrum analysis was conducted to verify whether fishing has influenced community structure. The results indicated contrasting seasonal patterns of deterministic processes in the downstream and lake sectors, suggesting that competition or abiotic factors may play a role in community structure. Stochastic patterns were recorded in the other sectors. Environmental factors, such as water transparency and depth, and the reservoir level were also closely related to the relative abundance of species in the communities. The relationship between the species richness and the biomass of predators and prey indicated that predation was an important determinant of community structure, which was interrupted by selective fishing. Despite the stochastic nature of most processes, deterministic factors were fundamental to the structure of the assemblages found in the downstream and lake sectors.

Keywords: co-occurrence, stochastic processes, deterministic size spectrum, predator-prey relationships.

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Introduction

A number of studies have suggested that some ecological communities are structured by random, rather than systematic processes [1], while the structure of others may be determined by species interactions [2] or environmental factors, such as local and regional processes that function as filters to mold community parameters [3–5]. Other studies have shown that biotic and abiotic factors combine to regulate the diversity and composition of species in a community, although the relative contribution of these processes is still poorly understood [6–10].

In the specific case of fish communities, the relative importance of different environmental variables is related to the scale of analysis. On a small scale, biotic factors may play an important role in the organization of the community, whereas, on a broader scale, biogeographic processes and abiotic factors may be more important, including anthropogenic modifications [5, 11]. Gotelli and Ulrich [3] emphasize the fact that community structure is a result of the simultaneous contribution of multiple factors, such as environmental gradients, competition, predation, and facilitation, which may have cumulative or opposing effects. Where the latter occur, no clear pattern may emerge.

The analysis of the co-occurrence of species has become a common practice in ecological studies that aim to understand the deterministic or stochastic patterns that underpin community structure, and the environmental factors that determine these patterns [12]. Null models simulate the behavior of communities in the absence of biological interactions (interspecific competition) that may affect their structure. Biological interactions, such as competition, will alter the random distribution of species predicted by null models, creating more systematic patterns [3, 13].

In many tropical aquatic ecosystems, predation is also a prime mover of community structure, affecting the species composition, abundance, and biomass of fish communities [14]. High predation rates may have profound knock-on effects throughout the trophic network, with restrictions on productivity [15, 16], and top-down control (predation) of the food chain may potentially lead to major changes in the biomass of the lower trophic levels in lacustrine ecosystems [17].

Fisheries also have an impact on fish community structure and composition, as well as on the food chain. Piscivorous and carnivorous fish are the primary target species of many commercial fisheries, and a reduction in the abundance of these species in the wild generally reflects the impact of the exploitation of fishery resources. This also has an effect on community structure [18].

In reservoirs, the modification of river dynamics caused by damming results in alterations in the local fish community, with the proliferation of species that are able adapt to the new conditions, and the decline or extinction of others that are less able to adapt [19–21]. While the long-term effects of this process may be relatively well-known, the factors that determine the structure of the community following damming are still poorly understood.

Coaracy Nunes, on the Araguari River in the state of Amapá, was the first reservoir built in the Brazilian Amazon region for the production of electricity, with construction beginning in 1967 [22]. At this time, environmental impact studies were not a legal requirement, and no scientific data were collected on the local fish community until the present study, conducted in 2008. As new dams are being built or planned for the Araguari, effective environmental management practices need to be put in place, and data from Coaracy Nunes are essential for the systematic assessment of the long-term effects of the impacts of damming. Given this, the present study analyzed the structure of the fish communities found within the area of the Coaracy Nunes reservoir, with the aim of identifying and evaluating the role of the different factors, both biotic and abiotic, in the configuration of the local assemblages. The study tested the hypothesis that the structure of the fish assemblages found in lotic environments is regulated by stochastic factors, while that of lentic habitats is governed by deterministic ones.

Methods

Study area

The study area is located in the middle sector of the Araguari River, in the area influenced directly by the Coaracy Nunes hydroelectric power station (UHE Coaracy Nunes), between latitudes 00°45’ N and 00°88’ N, and longitudes 51°13’ W to 51°20’ W. The Araguari is the principal river of the Brazilian state of Amapá, with a drainage basin of approximately 38,000 km², stretching between the Tumucumaque mountains, in the north, and the Atlantic Ocean, in the south, where it is influenced by the Amazon River [23].

The local terrain is mildly undulating, at altitudes of between 28 m and 65 m a.s.l. The climate is super-humid equatorial, with temperatures of between 20°C and 36°C, with the highest temperatures reached at the end of the day, between 17:00 h and 19:00 h, and the minimum temperatures recorded just after dawn, between 05:00 h and 07:00 h [24]. Mean relative humidity is 83.5% [24].

Annual precipitation is typically between 1500 mm and 3500 mm, with two well-defined seasons, a rainy season between mid-December and June, known locally as the “winter”, and a dry season, between July and mid-December, known as the “summer”. While the rainy season is characterized by frequent torrential downpours, precipitation is greatly reduced during the dry season, when the trade winds increase, intensifying between September and December. Historical records of the level of the river (Fig. 1) indicate a flood phase between January and June, which coincides with the rainy season, and a low water phase between July and December. The local vegetation is characterized by a mosaic of tropical rainforest, savanna, and swamp [24].

Four sectors were established for the present study (Fig. 1), representing four distinct environments: (i) downstream from the dam, an area characterized by lotic environments, with water flow being determined by the operation of the turbines in the dam, (ii) the reservoir proper, with semi-lotic conditions intermediate between those of the river and the lake, (iii) the lake area, adjacent to the reservoir, with lentic characteristics, and (iv) the upstream area, with lotic characteristics. Extensive deforestation is evident along the middle and upper margins of the reservoir and the upstream sector, while the other areas are relatively well-preserved. Gravel is also extracted from the upstream sector.

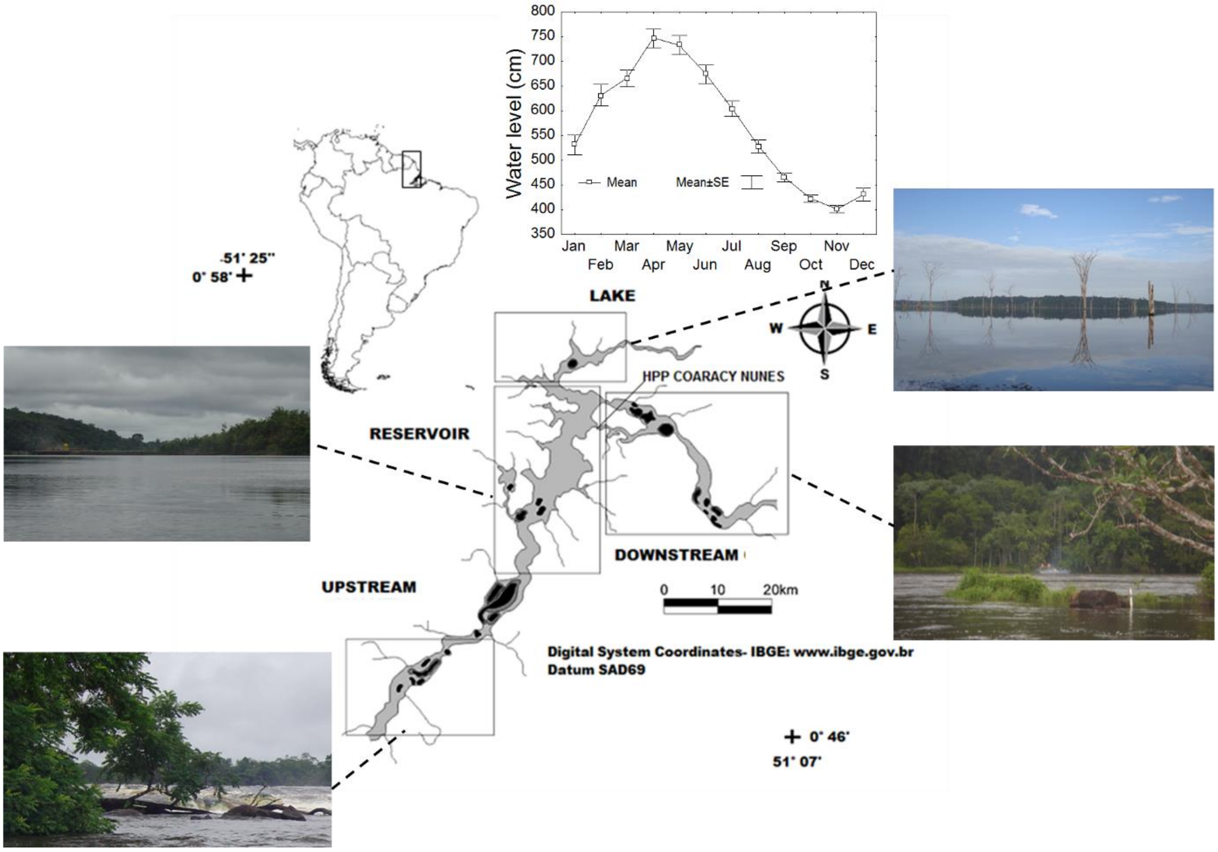

Fig. 1. Study area: the four study sectors (upstream, reservoir, lake, and downstream) located within the area of the Coaracy Nunes reservoir in Ferreira Gomes, Amapá, Brazil, and mean monthly variation in the water level (mean ± standard error, in cm) at Coaracy Nunes between 1952 and 2010.

Experiment design

Data were collected in each sector of the study area every two months between May, 2009, and July, 2010, with four samples representing the rainy season, and four, the dry season. Within each sector, seven areas of calm water were selected as sampling points for the collection of fish specimens, using gillnets, and the measurement of the physical-chemical parameters of the water – temperature (C°), pH, electrical conductivity (µS.cm^{-1}), dissolved oxygen (mg L^{-1}), transparency (m), and depth (m). All parameters except pH and transparency were recorded using a calibrated YSI-85 multi-analyzer, with pH being measured using an YSI-60 potentiometer, and transparency with a Secchi disk attached to a line graded in centimeters.

Precipitation (mm) and air temperatures (ºC) for the study period were obtained from the Coaracy Nunes meteorological station, together with data on river discharge and water levels. Data on the level of the Araguari River in the study area were obtained from the records from measuring station 22, available on the Brazilian National Waters Agency (ANA) website.

Standardized samples of the fish fauna were collected using seven sets of eight gillnets made of monofilament nylon with internode meshes ranging from 3 cm to 24 cm. Each set of nets was set at one of seven sampling points located within each sector, separated by a minimum distance of 500 m. The nets were 10 m – 40 m in length, and 1.5 m – 5.0 m in height, with a total area of 525 m² per set. The nets were set between 16:00 h and 09:00 h (a total of 17 hours), and fish were removed every four hours. Complementary sampling was conducted using equipment such as hand-lines, cast nets, trawls, and harpoons, to guarantee the most complete list of species possible for each sector.

Once retrieved, the specimens were stored on ice for identification, measurement, weighing, and photography, and then fixed in 10% formaldehyde for identification to the lowest possible taxonomic level. Identification was based on the specialist literature [25–29]. The classification was confirmed by Dr. Michel Jegú of the Musée de Histoire Naturelle in Paris, France, and voucher specimens were deposited in the Ichthyology and Limnology Laboratory at the Federal University of Amapá (UNIFAP) in Macapá.

Statistical analyses

Basic parameters were determined for each sector, including species richness [30], and relative abundance and biomass, based on the Capture per Unit Effort (CPUE), calculated by CPUE = (C/E) * 100, where C = number of individuals, for CPUEn (or total weight, in the case of biomass, CPUEb) captured, and E = sampling effort (m² of net by hours of sampling). In the present case, sampling effort was 525 m² of net in 17 hours.

Spatial and temporal variation in environmental parameters, species richness and CPUEb was evaluated using a two-way Analysis of Variance (ANOVA), considering $\alpha = 0.05$. The data analyzed using these procedures were first tested for normality (Kolmogorov-Smirnov and Shapiro-Wilk tests) and homoscedasticity of variance (Levene). When these assumptions were not upheld, the square root of the values was used for analysis. Differences detected in the ANOVA were verified by Tukey's *a posteriori* test to determine which pairs of sites were significantly different ($\alpha = 0.05$).

A multivariate BIOENV analysis was conducted to verify the influence of environmental factors on the spatial-temporal structuring of the local fish communities using measures of abundance (CPUEn) during the two seasons. This analysis identifies the parameters that contribute most to community structure. It is based on a multivariate comparison of the degree of agreement between the two matrices of biotic and abiotic similarity. The Bray-Curtis statistic was used for the biotic variables, and the normalized Euclidian distance for the abiotic variables [31]. All the multivariate analyses were run in PRIMER 6.0 [32].

A null model analysis was used to verify the existence of patterns of community structure related to biotic variables (competition, predation), abiotic or random factors. This analysis is based on the comparison of the indices of co-occurrence with the values estimated by the model. The occurrence of the species found in each sector was randomized [33] using EcoSim 7.0 [34], with the standardization of the data indicated by SIM09. The C score is an index which correlates negatively with the co-occurrence of species, and the observed score will be significantly higher than the expected one in communities structured by competitive interactions or abiotic factors. When the scores are lower than expected, community structure may be being affected by environmental affinities or facilitation. A random distribution may reflect the combined effects of a range of specific factors or simply, stochastic processes [7].

To evaluate the possible influence of predation on community structure, the species were classified according to their feeding habit as either (i) predators (piscivores, with a diet consisting primarily of other fish) or (ii) prey (species with non-fish diets) [35]. Linear correlations were run between the species richness of predator and prey, as well as their relative biomass (CPUEb). This analysis contributed to the evaluation of the effects of predation on fish biomass, and hence to community structure in the different sectors.

Analyses of the size spectrum were conducted in order to identify the possible effects of fisheries on community structure in the four sectors. For this, a linear regression of mean abundance per size class on mean body length, expressed as a Napierian logarithm, was calculated for the comparison of seasons and sectors. The parameters slope (b) and intersection (a) of the linear relationship between these variables reflect the intensity of fishery exploitation in the study area [36, 37].

Results

Environmental parameters

Mean river discharge was 328 m^3/s, ranging from 96 m^3/s in November 2009 to 396 m^3/s in May 2009, with a significant difference between seasons ($t = -4.92$; $p = 0.002$). The mean river level during the study period was 579.625 cm, varying from a low of 387.5 cm in November, 2009, to 678.5 cm in May, 2009. In this case, however, there was no significant seasonal difference ($t = -0.8815$; $p = 0.410$). Significant differences were found among sectors in all physical-chemical parameters except pH (Table 1).

Table 1. Meteorological and physical-chemical parameters recorded in the different sectors of the study area at UHE Coaracy Nunes during the study period. (Mean ± SD (minimum–maximum) value recorded in the sector).

Variable	Downstream	Reservoir	Lake	Upstream	ANOVA
Temperature (°C)	27.11±0.4 (26.52-27.75)	27.99±0.21 (27.75-3.5)	27.75±0.15 (27.50-27.95)	26.12±0.30 (25.73-26.60)	F = 86.382; p = 0.000
O_2 ($mg.L^{-1}$)	5.04±0,02 (5.01-5.06)	3.5±0.65 (3.19-5.11)	5.18±0.10 (5.00-5.30)	4.65±0.64 (3.22-5.03)	F = 742.430; p = 0.000
pH	4.64±0.25 (4.40-5.24)	4.68±0.28 (4.2-5.02)	4.80±0.27 (4.54-5.23)	4.38±0.63 (3.32-5.02)	F = 6.474; p = 0.056
Transparency (Secchi-m)	1.56±0.35 (1.13-2.13)	1.74±0.17 (1.55-1.98)	1.74±0.22 (1.48-2.08)	1.60±0.20 (1,18-1.82)	F = 3.035; p = 0.031
Conductivity (µS. cm^{-1})	19.33±0.19 (19.08-19.73)	22.4±0.59 (21.53-23.48)	18.43±0.17 (18.15-18.73)	18.41± 0.30 (18.05-18.90)	F = 271.598; p = 0.000
Depth (m)	3.69±0.31 (3.12-4.05)	7.23±1.94 (5.4-9.95)	7.23±0.55 (6.35-7.82)	4.81±0.90 (3.65-6.10)	F = 77.716; p = 0.000

Total monthly precipitation ranged from 7.3 mm to 475 mm, with the highest values being recorded between January and March, 2010, and the lowest in September and November, 2009. There was a significant difference ($t = -4.283$; $p = 0.004$) in monthly precipitation between the rainy (January–June) and dry (July–December) seasons, which was clearly related to the seasonal variation in fluvial discharge. Temperatures varied from 20.0°C to 33.5°C, with the highest monthly means being recorded in November, 2009, and March, 2010. In contrast to the precipitation pattern, no marked seasonal variation was recorded in ambient temperature ($t = -0.416$; $p = 0.690$).

Fish species

The total species richness recorded for the study area was 81 species. The lowest species richness was recorded during high water, and the highest during the low water period. Species richness varied considerably among the sectors, with 64 being recorded in the downstream sector, 40 in the reservoir, 33 in the lake, and 21 in the upstream sector (Appendix 1).

Total species richness varied between seasons in each of the different sectors. In the downstream sector, 49 species were recorded during high water, and 51 during low water, while in the reservoir, 31 and 32 species were registered at high and low water, respectively, 25 and 28 species were recorded in the lake, and 16 and 18 species in the upstream sector. Species richness varied significantly among sectors ($F = 27.375$; $p < 0.001$), with the greatest differences being found between the upstream and downstream sectors (Tukey: $p < 0.05$). Differences in species richness between the seasons were not significant for any of the sectors ($F = 0.005$; $p = 0.942$).

Total relative biomass (CPUEb) was 37.046 $g.m^{-2}.h^{-1}$, ranging from 17.885 $g.m^{-2}.h^{-1}$ during the flood period to 19.160 $g.m^{-2}.h^{-1}$ in the ebb. By weight, the CPUEs were 8.848 $g.m^{-2}.h^{-1}$ and 9.136 $g.m^{-2}.h^{-1}$ (in the flood and ebb periods respectively) in the downstream sector, 4.797 $g.m^{-2}.h^{-1}$ and 4.086 $g.m^{-2}.h^{-1}$ in the reservoir, 2.144 $g.m^{-2}.h^{-1}$ and 3.736 $g.m^{-2}.h^{-1}$ in the lake sector, and 2.094 $g.m^{-2}.h^{-1}$ and 2.200 $g.m^{-2}.h^{-1}$ in the downstream sector. Significant variation was found in the mean biomass among the sectors ($F = 6.380$; $p < 0.001$), with the most significant differences being found between the downstream sector and the lake and upstream sectors (Tukey: $P < 0.05$). No significant seasonal variation was found in relation to any parameter ($F = 1.213$; $p = 0.282$).

Co-occurrence of species

Significantly higher C scores ($p < 0.05$) were obtained for the downstream and lake sectors in the flood season when compared to the expected values (Table 2). This indicates that these communities have a deterministic structure, influenced by biological and/or environmental factors. No clear pattern was found in the other areas or periods.

Table 2. Observed and expected results for the C-Score index for the fish assemblages in the area of the UHE Coaracy Nunes reservoir.

	C score			
Sector/period	**Observed**	**Expected**	**SD-expected**	**(*p:*obs > exp)**
Downstream/flood	1.76	1.76	0.00117	0.530
Downstream/dry	1.53	1.50	0.00007	**0.001**
Reservoir/flood	1.34	1.33	0.00038	0.280
Reservoir/dry	1.35	1.36	0.00053	0.690
Lake/flood	1.11	1.08	0.00067	**0.010**
Lake/dry	1.08	1.08	0.00780	0.500
Upstream/flood	0.97	0.95	0.00130	0.340
Upstream/dry	1.26	1.24	0.00645	0.250

Statistically significant correlations: $P < 0.05$

Environmental versus biological parameters

The BIO-ENV analysis recorded strong correlations between the CPUEn values and different environmental parameters recorded in the study area (Table 3). During both seasons, the strongest correlations were found in the reservoir sector, and the weakest in the lake. In the reservoir and downstream sectors, the same combination of variables was recorded in both seasons, whereas in the lake, distinct patterns were recorded in the two seasons, and there was a difference in the relative influence of the variable in the upstream sector. Even so, correlations were strongest in the lake sector, and weakest in the reservoir, especially during the ebb period. Overall, the environmental factors that correlated most consistently with the biological variables were transparency, depth, water level, precipitation, and river discharge.

Size spectrum

The down- and upstream sectors were characterized by the shallowest regression slopes (b) in the size spectrum analysis, which indicated the presence of larger individuals than in the other two sectors (Table 4). In the specific case of the downstream sector, all the intercepts (a) were significantly different from zero ($p < 0.05$), which was not the case for the slopes. A similar pattern was recorded for the reservoir and upstream sectors. In the case of the lake community, both “a” and “b” were significantly different during the dry season, but during the rainy season, only “a” varied significantly, diverging from the seasonal pattern recorded in the other areas. In the reservoir, the steepest slope (b) was recorded in the rainy season (Table 4).

Predator versus prey species

The total number of predator species in each sector was smaller than that of prey. In the downstream sector, there were 21 species of predator and 37 of prey, 17 and 20 species, respectively, in the reservoir sector, 14 and 17 in the lake sector, and nine and 11 in the downstream sector. The richness of predator species varied significantly among sectors (F = 6.751, p = 0.006), with the greatest difference being found between the upstream sector and the reservoir and downstream sectors (Tukey: p < 0.05). The richness of prey species was also significantly different between the downstream assemblage and those of all other sectors (F = 11.126, p < 0.001; Tukey < 0.05).

Table 3. Seasonal variation in the relationship between the relative abundance of fish (CPUEn) in the different sectors of the Coaracy Nunes reservoir and environmental variables, based on Spearman correlation coefficients.

Sector/period	N° of variables	r_s	Combination
Downstream/flood	1	0.314	Transparency
	2	0.600	Transparency, discharge
	3	**0.771**	Transparency, discharge, precipitation
Downstream/dry	1	0.486	Transparency
	2	**0.829**	Transparency, discharge*
	3	0.771	Transparency, discharge, precipitation
Reservoir/dry	1	0.486	Water level
	2	**0.600**	Water level, precipitation
	3	0.200	Water level, precipitation, depth
Reservoir/dry	1	0.086	Water level
	2	0.086	Water level, precipitation
	3	0.200	Water level, precipitation, depth
Lake/flood	1	0.829	Precipitation
	2	0.886	Precipitation, depth
	3	**0.943**	Precipitation, depth, discharge*
Lake/dry	1	0.714	Transparency
	2	0.771	Transparency, depth
	3	**0.829**	Transparency, depth, water level*
Upstream/flood	1	0.714	Depth
	2	**0.886**	Depth, water level
	3	0.543	Depth, water level, discharge
Upstream/dry	1	0.600	Depth
	2	0.657	Depth, discharge
	3	**0.714**	Depth, discharge, water level*

Statistically significant correlations:* ($P < 0.05$)

Table 4. Results of the size spectrum analysis (log–log regression of relative abundance on size classes) showing the slope (*b*) and intercept (*a*) with their respective standard errors for the fish assemblages of the different sectors of the area of influence of the Coaracy Nunes reservoir in Amapá, Brazil.

Sector		Value recorded during the flood –Dry periods in sector:							
		Downstream		Reservoir		Lake		Upstream	
		Flood	Dry	Flood	Dry	Flood	Dry	Flood	Dry
Slope	*b*	-1.55	-2.65	-1.05	-1.00	-0.88	-1.42	-1.85	-3.93
	St. error	1.53	1.42	0.68	0.65	0.81	0.53	2.01	1.78
	t	-1.05	-1.85	-1.52	-1.53	-1.08	-2.65	-0.92	-2.2
Intercept	*a*	4.83	5.91	3.63	3.59	3.47	3.84	3.72	3.89
	St. error	1.15	1.19	0.29	0.34	0.36	16.22	0.37	0.36
	t	4.18	4.96	12.3	10.51	9.51	4.69	9.84	10.8
Adjust to Model	*F*	1.00	3.45	2.32	2.34	1.18	7.06	0.85	4,86
	R^2	0.11	0.3	0.32	0.36	0.22	0.58	0.14	0.54
	p	0.34	0.09	0.18	0.20	0.33	0.04	0.39	0.09

The relative biomass of predators was higher than that of prey in the upstream and reservoir sectors, as well as the downstream sector during the flood period (Fig. 2). In the lake and downstream sectors, by contrast, the relative biomass of prey species was higher than that of the predators. Predator biomass was significantly higher in the downstream sector than in the reservoir, lake, and upstream sectors (Flood: F = 4.686; p = 0.022; Tukey < 0.05; Dry: F = 4.683; p = 0.022; Tukey < 0.05). For prey species, significant differences (F = 6.379; p = 0.007) were found between the downstream and upstream assemblages during the dry season (Fig. 2).

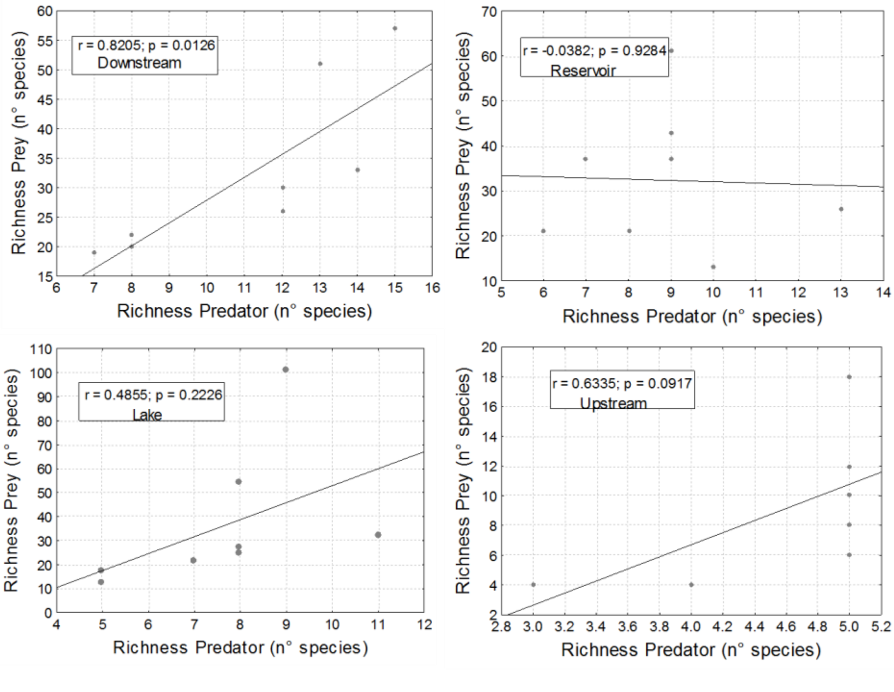

Fig. 2. Seasonal variation in the relationship between predator and prey species richness (S) in the fish assemblages of the four sectors of the Coaracy Nunes study area in Amapá, Brazil.

There was a positive correlation between predator and prey species richness in the majority of the fish assemblages found within the area of the Coaracy Nunes reservoir, except for the reservoir during the dry season, and the upstream area during the flood periods. In both these cases, a negative correlation was found (Fig. 3). These correlations (Pearson's *r*) varied from medium to very strong, reflecting the role of predation on community structure.

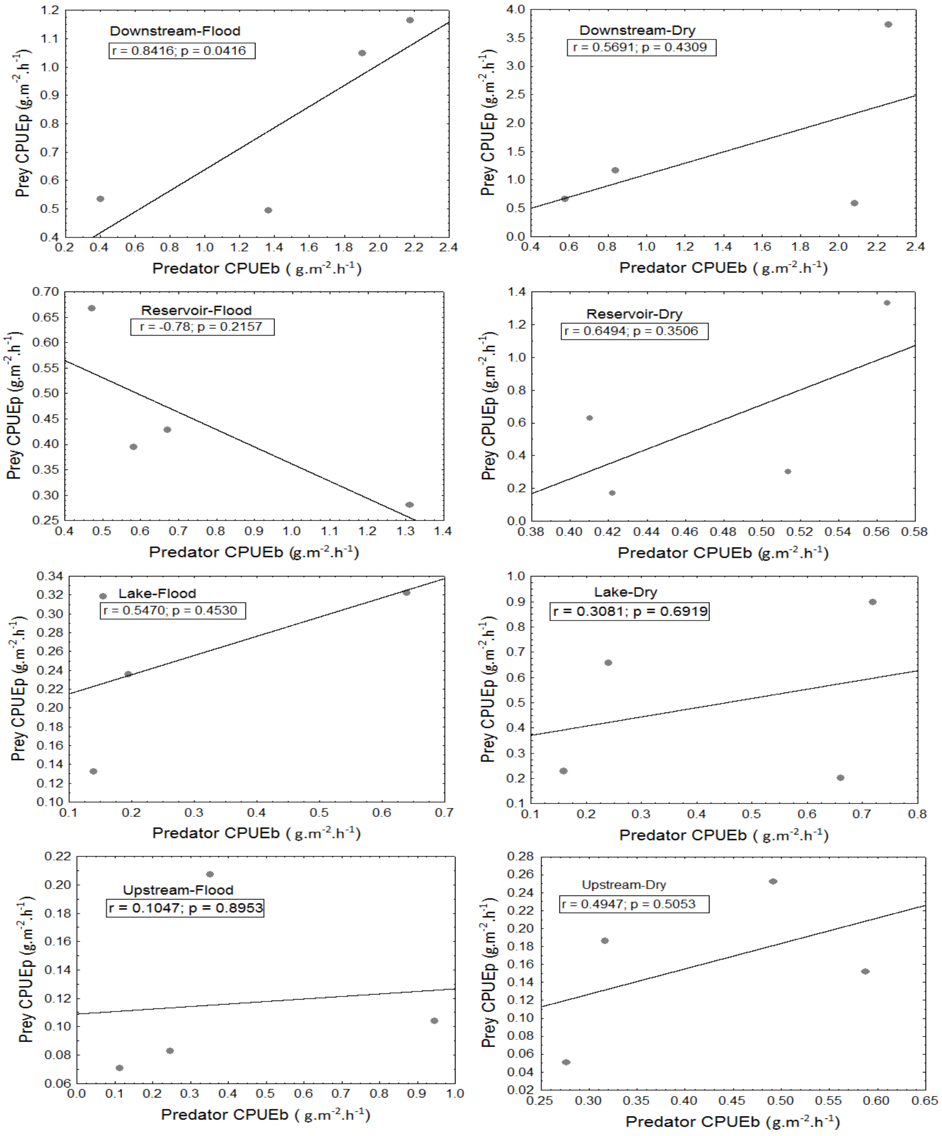

Fig. 3. Seasonal variation in the relationship between predator and prey species relative biomass (CPUEb) in the fish assemblages of the four sectors of the Coaracy Nunes study area in Amapá, Brazil.

The relative biomass of predators was related positively to that of prey species in all the assemblages, and in both seasons, which indicates that prey biomass was adequate for the maintenance of the local predator biomass, irrespective of the seasonal conditions. Given this, predation has a fundamental effect on the organization of the communities found in all the areas to a greater or lesser extent (Fig. 2 and 3).

Discussion

No significant temporal variation was observed in the physical-chemical parameters of the water anywhere within the study area, nor did water levels or air temperatures vary significantly among sectors or between seasons. However, the depth of the water, river discharge, and rainfall varied significantly among sectors and between seasons. These fluctuations in depth and discharge resulted from greater input of rainfall run-off during the rainy season than in the dry season, as well as the daily adjustment of the reservoir level through the regulation of the dam gates and abductor channels to guarantee the functioning of the turbines. This led to not only seasonal, but also daily variation in the water level of all four sectors, and in particular the occasional drying out of the downstream sector. In fact, the daily variation in water level may exceed the seasonal amplitude and have a profound effect on the physical-chemical characteristics of the water which may. in turn, affect biological productivity [20, 38, 39].

Species richness was considerably lower in the reservoir (40 species), lake and upstream sectors (21 species) compared to the downstream sector (66 species). Sá-Oliveira *et al.* [40] recorded an additional 40 species (a total of 106) in the downstream sector using a variety of fishing methods. This comparison indicates that the construction of the dam has had a negative influence on all the upstream fish communities, including those of the reservoir, but not on the downstream area. A similar situation has been found in other Amazonian hydroelectric schemes, such as Curuá-Una [41], Tucuruí [41], Balbina [42], and Samuel [43], as well as at sites in other Brazilian regions [44–47]. Agostinho *et al.* [20] review of the data from 77 Brazilian reservoirs which revealed that most contained fewer than 40 species, similar to the findings of the present study.

In addition, the higher levels of abundance recorded in the lake and reservoir were due to the capture of small-bodied species, such as *Hemiodus unimaculatus, Psectrogaster* af. *falcata, Charax gibbosus, Geophagus proximus*, and *Serrasalmus gibbus*, common omnivores and carnivores in lacustrine environments. The presence of these species may be related to the modification of the lotic environment to a semi-lotic and lentic one, as observed at Curuá-Una [41] and other reservoirs [48].

The relative abundance of fish in the downstream area was low compared to that recorded in the lake and reservoir. However, the fauna in the downstream area presented the most balanced distribution of abundance among species, except in the case of *Hemiodus unimaculatus*, for which the higher CPUEn value was related to its habit of forming shoals, especially during the breeding season, thus increasing the abundance of the species during sampling. *Vieira et al.* [41] also recorded a relative abundance of hemiodontids in the Curuá-Una reservoir, due to the formation of shoals by these fish. The lowest relative abundances were recorded in the upstream area, where *Ageneiosus ucayalensis, Leptodoras* sp., and *Serrasalmus gibbus* were the most common species in the samples. In addition to the effects of the quality of the environment in the different zones of the study area, a number of factors contributed to the observed pattern, such as sampling effects, related to the morphological characteristics of the study area.

The highest relative biomass was recorded in the downstream area, and was influenced primarily by the contribution of *Boulengerella cuvieri* and *Ageneiosus ucayalensis*. The high biomass recorded in the reservoir was influenced by the large-bodied species, such as *Ageneiosus ucayalensis*, as well as the small- to medium-sized species, like *Hemiodus unimaculatus, Serrasalmus gibbus*, and *Geophagus proximus.*

The higher relative biomass recorded for a single species in the lake sector was for *Curimata inornata*. This bentho-pelagic detritivore forms large schools for trophic and breeding migrations [49]. The limnological characteristics of the lake sector are similar to those of an oligotrophic lake, with high transparency and low primary productivity, fed primarily by the input of allochthonous material [49], which favors detritivorous species such as *C. inortata*.

The co-occurrence analysis indicated that species were distributed randomly in the reservoir, lake, and upstream sectors in both seasons, indicating that the structure of the respective communities was determined by stochastic factors. In the downstream sector during the ebb period, by contrast, and in the lake during the flood, more deterministic patterns of community structure were observed, indicating the influence of biological interactions and/or environmental factors.

In the downstream sector, this process may be associated with the reduction of the river's discharge during the dry season, which led to a decrease in the flooded area, concentrating the species into a smaller area and intensifying their interactions, either competitive and/or predatory. Under these conditions in limnetic systems, biological processes may have an even stronger influence on the distribution of organisms than environmental variables, or even the combined effects of habitat heterogeneity and resource partitioning. The simultaneous influence of these factors reduces competition between species and facilitates their coexistence [50–52]. Huston [53] concluded that the intensity of the disturbance provoked by the annual fluctuations in river level and competitive exclusion are the fundamental factors controlling species diversity. The pattern observed in the lake sector during the flood period may have been related to the lentic characteristics of this environment, as well as its reduced area, which may have intensified the interaction between biotic and abiotic factors on a local scale, as observed by Huston [53].

A number of studies have demonstrated that the variation in hydrological features is one of the principal determinants of community structure in lotic environments [54–56], and that local processes – limnological and structural aspects of the habitat and intra- and inter-specific interactions – are the primary factors determining variations in community structure among habitats or geographical areas. However, it is normally difficult to determine which factors are the most important [40].

The composition of local communities may be determined by a combination of both stochastic and deterministic processes, including the combined effects of environmental gradients, competition, predation and facilitation [57–59]. As many of these factors may have contrasting effects, the end result may lack any systematic spatial pattern [3]. In our study, the results of the BIO-ENV indicated that abundance was related primarily to the depth of the reservoir, discharge, transparency, and rainfall levels. However, most processes were more stochastic, and systematic patterns were observed only in the downstream sector during the dry season and in the lake sector. The reduced variation in the level of the reservoir over the course of the year contributed to the stability of the reservoir and lake sectors, with daily fluctuations occurring in all sectors due to the operational adjustments of the level of the reservoir, which may have been responsible for variation on a localized scale.

The operational adjustments of the reservoir level interfere in the flood-ebb cycle of the river and modify the synchrony of the reproductive patterns of most fish species. Even where synchrony is upheld, the short duration of the flood period may impede the development and recruitment of the juveniles, affecting community structure [60, 61]. This artificial modification of the hydrological cycle may cause a certain amount of disorganization in the local communities at all levels. Similar scenarios have been observed in other reservoirs, indicating that the modification of the hydrological cycle and, in particular, the occurrence of unpredictable flood pulses, may result in a continuous reorganization of the local fish communities [30, 63, 64]. Moderate levels of disturbance may nevertheless maximize the diversity of habitats and, as a consequence, species diversity [65], but it may also affect major biotic interactions and have a negative effect on diversity [66].

In addition to the seasonal fluctuations in the hydrological regime, habitat heterogeneity, and predation, a number of other fundamental factors, such as topography, geomorphology, and specific features of the environment's hydrodynamics, such as river width and depth, discharge, and substrate types, may also have a profound effect on fish community structure [67, 68]. In lakes, the principal factor determining community structure is the flood pulse [60, 61]. In particular, seasonal variations in the depth of the water can have fundamental effects on the whole community by affecting the availability of feeding resources, breeding areas, and refuges [69].

Our study confirmed the role of predation in community structure, with a strong correlation between the species richness of predators and prey throughout the year, albeit with a negative relationship in the reservoir sector during the dry season, and the upstream sector during flood periods. The abundance of piscivorous species, such as *Ageneiosus ucayalensis*, *Serrassalmus gibbus*, and *Acestrorhynchus falcirostris*, which are well adapted for survival in waters with strong currents, as well as others of the genus *Hoplias*, together with the plentiful numbers of prey species, like *Hemiodus unimaculatus* and *Curimata inornata*, and other detritivores and omnivores, may be contributing to the equilibrium in the predator-prey relationships within the community, and the structure of the local assemblages.

The positive correlation between the biomass of predator and prey species in the assemblages of the different sectors reflects the role of predation pressure in the control of prey biomass. However, the moderate scores obtained for these correlations indicates that other factors influence this relationship, such as the distribution of abundance and biomass of prey species within each sector, in particular during the dry season. During this period, the reduction in the flooded area results in a concentration of individuals, intensifying the interactions among species, as well as the effects of environmental factors. During the flood period, by contrast, the environmental conditions are more favorable for reproduction for most species, resulting in an overall increase in biomass, and the recuperation of stocks for the dry season. Ward *et al.* [70] refer to the dry season as the “biological interaction phase”, due to the reduction in physical space and the availability of habitats, which is counterbalanced by an increase in the density of individuals and species, resulting in the intensification of intra- and inter-specific interactions.

A number of experimental studies have found evidence that predation has a clear and predictable effect on the structure of prey fish populations [14, 35]. High levels of predation pressure may have a marked effect on the whole trophic network, including community structure [20, 48]. The reduced abundance of macrophytes in the study area may also have contributed to community structure, given that these plants provide a number of different species with sites for feeding, refuge, and breeding [71].

Ultimately, the pressure exerted by fisheries may also be considered an important determinant of community structure in both natural and anthropogenic environments. The analysis of the size spectrum presented here indicated that the populations in all the study sectors were consistent with the linear model, in which abundance declines gradually with increasing body size. During the dry season, slopes were steeper, reflecting the removal of the larger individuals with a higher economic value. These large individuals, which are captured selectively, are normally either predators or large-bodied herbivores, such as *Cichla* sp and *Tometes* sp. This results in a decrease in predation levels and a consequent increase in the abundance of prey and competition among these species. The more intense the pressure from fisheries, the steeper the slope and the intercept of the size spectrum. This occurs even where some species are migratory (Isaac, 2011, personal observation).

Implications for conservation

The results of the present study uphold the proposed hypothesis that the characteristics of the fish assemblages of the area influenced by the dam are affected by both random and deterministic factors. Differences between these two processes depend on the type of environment formed by the damming of the river, as well as its degree of isolation. Where space is limited, community structure is affected strongly by deterministic forces, such as abiotic variables and biological interactions (competition and predation). By contrast, in more open habitats, such as the up-and downstream sectors of the river, which present fewer barriers to dispersal, community structure tends to be affected by stochastic processes. However, when these lotic habitats become more isolated, the influence of deterministic factors will tend to increase.

The Araguari is one of the most important Amazonian rivers. Its headwaters lie in the Tumucumaque Mountains National Park, on the Guianan plateau, and much of its course lies within this conservation unit. The construction of new hydroelectric dams along this river is impacting the natural environment and its biota, in particular its fish populations (Sá-Oliveira et al, 2015). The present study has contributed to the understanding of these impacts, and provides important insights for the development of effective conservation measures and management strategies that can mitigate the impacts of the damming of the Araguarí, and may help ensure the maintenance of well-balanced and functional ecological communities over the long term.

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Appendix 1. Fish species, their diet and status, and their maximum length (Lt cm) in the different sectors of the study area at UHE Coaracy Nunes during the study period.

	Maximum length (cm) in:					
Taxa	Downstr.	Reserv.	Lake	Upstr.	Diet	Status
Acestrorhynchus falcatus (Bloch, 1794)	19.7				Piscivore	Predator
Acestrorhynchus falcirostris (Cuvier, 1819)		30.6	30.1	24.5	Piscivore	Predator
Ageneiosus inermis (Linnaeus, 1766)	58.7	47.0	20.0		Piscivore	Predator
Ageneiosus ucayalensis (Castelnau, 1855)	28.9	54.0	46.8	31.0	Piscivore	Predator
Auchenipterus nuchalis (Spix & Agassiz, 1829)		10.8	22.5		Piscivore	Predator
Auchenipterus osteomystax (Miranda Ribeiro, 1918)	20.0				Piscivore	Predator
Bivibranchia notata (Vari & Goulding, 1985)	19.5		16.4		Omnivore	Prey
Boulengerella cuvieri (Agassiz, 1829)	80.4	67.3	69.5	38.5	Piscivore	Predator
Brachyplatystoma filamentosum (Lichtenstein, 1819)	101.0				Piscivore	Predator
Brachyplatystoma rousseauxii (Castelnau, 1855)	53.2				Piscivore	Predator
Bryconops caudomaculatus (Günther, 1864)	14.9	11.9	11.0		Omnivore	Prey
Charax gibbosus (Linnaeus, 1758)	22.5	14.0	19.0		Piscivore	Predator
Cichla monoculus (Spix & Agassiz, 1831)		51.1	20.5		Piscivore	Predator
Cichla ocellaris (Bloch & Schneider, 1801)		52.4	29.0		Piscivore	Predator
Colossoma macropomum (Cuvier, 1818)		53.5			Omnivore	Prey
Crenicichla strigata (Günther, 1862)	21.7				Piscivore	Predator
Curimata inornata (Vari, 1989)	31.7	31.0	31.7	20.0	Detritivore	Prey
Curimata sp. (Linnaeus, 1766)	27.8				Detritivore	Prey
Curimatella dorsalis (Eigenmann & Eigenmann, 1889)		11.3			Detritivore	Prey
Cyphocharax gouldingi (Vari, 1992)	12.6	12.6	12.3		Detritivore	Prey
Dekeyseria amazônica (Rapp Py-Daniel, 1985)	13.6				Detritivore	Prey
Electrophorus electricus (Linnaeus, 1766)		66.4		92.1	Carnivore	Predator
Geophagus proximus (Castelnau, 1855)	22.5	25.1	24.0		Omnivore	Prey
Glyptoperichthys joselimaianus (Weber, 1991)	20.8	26.0			Detritivore	Prey
Harttia duriventris (Rapp Py-Daniel & Oliveira, 2001)	21.4				Detritivore	Prey
Hemiodus microlepis (Kner, 1858)	27.8	19.1	24.2		Omnivore	Prey
Hemiodus quadrimaculatus (Pellegrin, 1908)	25.3	22.0			Omnivore	Prey
Hemiodus unimaculatus (Bloch, 1794)	23.5	25.0	24.0	25.8	Omnivore	Prey
Hoplerythrinus unitaeniatus (Agassiz, 1829)	17.0				Piscivore	Predator
Hoplias aimara (Valenciennes, 1847)	55.7	37.5	60.0	59.5	Piscivore	Predator
Hoplias macrophthalmus (Pellegrin, 1907)	89.3	62.0			Piscivore	Predator
Hoplias malabaricus (Bloch, 1794)		36.0	39.4		Piscivore	Predator
Hoplosternum litoralle (Hancock, 1828)	23.0				Omnivore	Prey
Hypophthalmus marginatus (Valenciennes, 1840)			16.2		Detritivore	Prey
Hypostomus emarginatus (Valenciennes, 1840)	27.0				Detritivore	Prey
*Hypostomus plecostomus (*Linnaeus, 1758)	27.3	24.3	26.4	26.5	Detritivore	Prey
Laemolyta petiti (Géry, 1964)				17.7	Omnivore	Prey
Leporinus af. parae (Eigenmann, 1908)	30.0	24.2			Omnivore	Prey
Leporinus affinis (Günther, 1864)	27.2	37.6	33.5	22.5	Omnivore	Prey
Leporinus maculatus (Müller & Troschel, 1844)	19.5				Omnivore	Prey
*Leptodoras sp. (*Günther, 1868)				25.6	Omnivore	Prey

	Maximum length (cm) in:					
Taxa	Downstr.	Reserv.	Lake	Upstr.	Diet	Status
Megalonema platycephalum (Eigenmann, 1912)	23.0	22.5			Piscivore	Predator
Metynnis lippincottianus (Cope, 1870)	18.0	7.5	11.9		Herbivore	Prey
Moenkhausia chrysargyrea (Günther, 1864)	14.8		8.2		Omnivore	Prey
Moenkhausia oligolepis (Günther, 1864)				8.4	Omnivore	Prey
Mylesinus paraschomburgkii (Jégu, Santos & Ferreira, 1989)	34.5				Herbivore	Prey
Mylesinus paucisquamatus (Jégu & Santos, 1988)	21.5				Herbivore	Prey
Myleus rhomboidalis (Cuvier, 1818)	44.5			38.1	Omnivore	Prey
Myleus rubripinnis (Müller & Troschel, 1844)	30.5				Herbivore	Prey
Mylossoma duriventre (Cuvier, 1818)	28.0				Omnivore	Prey
Osteoglossum bicirrossum (Cuvier, 1829)	69.3				Piscivore	Predator
Pachypops fourcroi (La Cepède, 1802)	14.5		17.2		Piscivore	Predator
Parauchenipterus galeatus (Linnaeus, 1766)		20.0		15.5	Carnivore	Predator
Parauchenipterus sp. (Kner, 1858)	24.0				Carnivore	Predator
Peckoltia oligospila (Günther, 1864)	22.5				Detritivore	Prey
Pellona castelnaeana (Valenciennes, 1847)	32.5				Carnivore	Predator
Pellona flavipinnis (Valenciennes,1836)	15.7				Carnivore	Predator
Piaractus brachypomus (Cuvier, 1818)	55.5				Omnivore	Predator
Pimelodella cristata (Müller & Troschel, 1848)		23.0			Carnivore	Predator
Pimelodus blochii (Valenciennes, 1840)	24.5	24.1	22.2		Omnivore	Predator
Pimelodus ornatus (Kner, 1858)	39.5	31.5	38.5	30.0	Piscivore	Predator
Plagioscion auratus (Castelnau, 1855)	22.0				Piscivore	Predator
Plagioscion squamosissimus (Heckel, 1840)	41.6				Piscivore	Predator
Platynematicthys notatus (Jardine, 1841)	39.0				Piscivore	Predator
Psectrogaster af. falcata (Eigenmann & Eigenmann, 1889)	21.7	32.7	33.5	22.8	Detritivore	Prey
Pseudacanthicus spinosus (Castelnau, 1855)	32.5				Detritivore	Prey
Pygopristis denticulata (Cuvier, 1819)	10.9				Carnivore	Predator
Retroculus lapidifer (Castelnau, 1855)	29.5				Omnivore	Prey
Roeboides affinis (Günther, 1868)	20.3	16.4	15.8	13.5	Piscivore	Predator
Satanoperca acuticeps (Heckel, 1840)	18.5	18.0	11.2		Omnivore	Prey
Schizodon vittatus (Valenciennes, 1850)	19.5				Herbivore	Prey
Serrasalmus elongatus (Kner, 1858)	24.1				Carnivore	Predator
Serrasalmus gibbus (Castelnau, 1855)	35.0	25.0	20.0	22.0	Carnivore	Predator
Serrasalmus rhombeus (Linnaeus, 1766)	41.2	32.0	33.5	43.0	Carnivore	Predator
Sternopygus macrurus (Bloch & Schneider, 1801)			39.0		Carnivore	Predator
Tetragonopterus chalceus (Spix & Agassiz, 1829)		22.5			Omnivore	Prey
Tometes trilobatus (Valenciennes, 1850)	46.0	47.6			Herbivore	Prey
Triportheus albus (Cope, 1872)	17.0				Omnivore	Prey
Triportheus angulatus (Spix & Agassiz, 1829)		25.3	23.3	22.0	Omnivore	Prey
Triportheus auritus (Valenciennes, 1850)	21.6	23.0	23.0	24.0	Omnivore	Prey
Triportheus trifurcatus (Castelnau, 1855)	21.9				Omnivore	Prey