



Mixed food web control and stability in a Cerrado river (Brazil)

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Abstract. Understanding the mechanisms which regulate aquatic food webs dynamics have been an important focus inquiry since ecological research started to emphasize ecosystems' structure and functioning. The objective of this study was verify if species composition were the same at three different habitats in Corrente River. If species composition were the same it will allow to model the food web by a single model, otherwise each portion should be modeled independently. Ecopath model and the keystone index (KSi) were used in order to evaluate the entire food web and to comprehend the system control. Five surveys in the period from June of 2003 to until June of 2005 were carried out in three different habitats in the river. Results showed that: i) there are seven fish species; ii) habitats are very similar; iii) all species reproduced in the rainy season with exception of *Brycon nattereri*. A single Ecopath model indicated low resilience and stability. Keystone rank values showed a mixed system control mechanism, where one predator, *Salminus hilarii*, one intermediate consumer, *Astyanax altiparanae* and one consumer of trophic level two (terrestrial invertebrates) had respectively, the highest keystone index values.

Key words: Paraná River, reproduction, feeding behavior, food web mechanisms, Corrente River

Resumo: Controle misto de teia trófica e estabilidade num rio de cerrado. O entendimento dos mecanismos que regulam a dinâmica das teias tróficas aquáticas tem sido um importante tópico desde que a pesquisa ecológica passou a enfatizar a estrutura dos ecossistemas. O objetivo deste estudo foi verificar se a composição das espécies de peixes era a mesma em três diferentes habitats num trecho do Rio Corrente (GO), e se fossem as mesmas, isto permitiria avaliar a teia trófica num único modelo, pois do contrário, seriam necessários um modelo para cada habitat. O modelo Ecopath e o índice de ranking de espécies-chave foram usados para avaliar a teia trófica e entender os mecanismos de controle do sistema. Cinco amostragens no período de junho de 2003 até junho de 2005 foram realizadas em três diferentes habitats ao longo do Rio Corrente. Os resultados mostraram que: i) há apenas sete espécies de peixes; ii) há alta similaridade entre os habitats; iii) todas as espécies se reproduziram na estação chuvosa, com exceção de *Brycon nattereri*. Um modelo Ecopath indicou que o sistema tem baixa resiliência e estabilidade. O ranking de espécies chave mostrou que o controle do sistema é misto, com um predador, *Salminus hilarii*, ou consumidor intermediário, *Astyanax altiparanae* e um consumidor de nível trófico dois (invertebrados terrestres) apresentando, respectivamente os maiores valores de índices de espécie-chave.

Palavras-chave: Rio Paraná, reprodução, hábito alimentar, controle de teia trófica, Rio Corrente.

Introduction

Limnological features and heterogeneity of micro-habitats affect fish species diversity and abundance at lotic ecosystems in overall world (Meffe & Sheldon 1988, Castro & Casatti 1997, Suárez & Petrere 2007). Similarly, terrestrial ecosystems such as riparian forest have direct

influence upon ichthyological diversity since it supplies shading, food (insects, seeds, fruits) and allochthonous material that contribute for the micro-habitats structure into the river (Cetra & Petrere 2007). In addition, fish species composition can be influenced by its own mechanisms which regulates dynamic of food webs, trophic structure and patterns

of energy flow (Angelini *et al.* 2006).

One approach towards understanding the food web dynamics has been to evaluate mechanisms which regulate the growth and development of aquatic food webs such as: i) resource limitation or bottom-up control, ii) predation or top-down mechanisms, iii) interaction of these mechanisms or mixed control (Forrester *et al.* 1999) or iv) wasp-wait, when a intermediate trophic level specie is fundamental for their predators and preys (Cury *et al.* 2000, Hunt Jr. & McKinnell 2006).

In this sense, identifying keystone species, i.e., those species that despite relatively low biomass have a structuring role in food webs, can be crucial for the comprehension of controlling mechanisms of the system maturity (Libralato *et al.* 2006). Besides the food web mechanisms, reproductive activity is another fundamental biotic process for keeping populations viability (Bailly *et al.* 2008).

Recently, the utility of ecotrophic models when managing fisheries and aquatic conservation has been established mainly by quantifying food webs through Ecopath software (Christensen *et al.* 2005, Hakanson & Gyllenhammar 2005, Angelini & Moloney 2007, Shannon *et al.* 2009). Despite its wide use in many habitats, Ecopath models have been scarcely applied to describe food webs in tropical rivers.

The present work aimed verify if species composition were the same at three different habitats along 28 km of a Cerrado's river. If species composition were the same it will allow modelers to describe the food web by a single model, otherwise each portion should be modeled independently. Ecopath model and the keystone index (KSi) were used in order to evaluate the entire food web and to comprehend the system control.

Material & Methods

Study area. The Corrente River it is located in the Paraná River Basin, in a drainage area of about 8000 km² and flows into Paranaíba River at 225 km downstream the studied area between Ilha Solteira and São Simão reservoirs.

The studied section of the Corrente River (Fig. 1) stretch for 28 km and it has fast flowing and two waterfalls with 4 and 25 meters height each. This stretch is partially covered by several vegetal formations such as gallery forest, alluvial woods and Cerrado, regardless of there is a predominance of antropogenic areas covered by pastures and farmland. There are no fishing activities in the river.

Fish sampling. Sampling was conducted at

eight sample points during one week at different seasons: 05/2003 (dry season), 09/2004 (dry), 12/2004 (rainy), 03/2005 (rainy) and 06/2005 (dry; Fig. 1). Two sets of eight gillnets of different mesh sizes and 10 meter long were used (12, 15, 20, 25, 30, 40, 50 and 60mm between opposing knots and ten meters long). The soak times were 24 hours and the checking happened in the morning (6:00 am) and in the evening (6:00 pm).

Three habitats (main channel, lentic areas and tributaries) were sampled aiming to verify the species composition similarity through Morisita (C_H) index (Magurran 2004).

After had been harvested, fish were separated in plastic bags and sent to a field laboratory in order to be conserved in ethylic alcohol 70°GL (Hahn *et al.* 1998) and be sent for taxonomic identification. Collected fishes were deposited in Ichthyological Collection of Laboratory of Science Education and Ecological Research, at State University of Goiás (Anápolis-GO).

Reproduction. Gonad development was determined taking into account macroscopic characteristics (described in Agostinho *et al.* 1993). Aiming to assess the reproductive activity, a classification according to the percentage of individuals in reproductive stage was defined resulting into four groups: incipient, moderate, intense and very intense.

Feeding information. Gut content of fish species were analyzed under a stereophonic microscope to identify up to the lowest taxonomic level possible, according to suitable methodology (Hellowell & Abel, 1971). The food index - IAI (Kawakami & Vazzoler, 1980) described below was used to quantify gut content:

$$IAi = \frac{F_i * V_i}{\sum_{n=1}^n (F_i * V_i)} \quad (1)$$

where:

i = 1,2...n= feeding item;

F_i = item occurrence frequency (%);

V_i= item volume (%);

Diet information from literature was used to *Hypostomus strigaticeps* (Cardone *et al.* 2006) while field observations and model automatic balance mass routine from Ecopath software were used to determine the proportion of fish consumption by two other species (*Salminus hilarii* and *Hoplias malabaricus*).

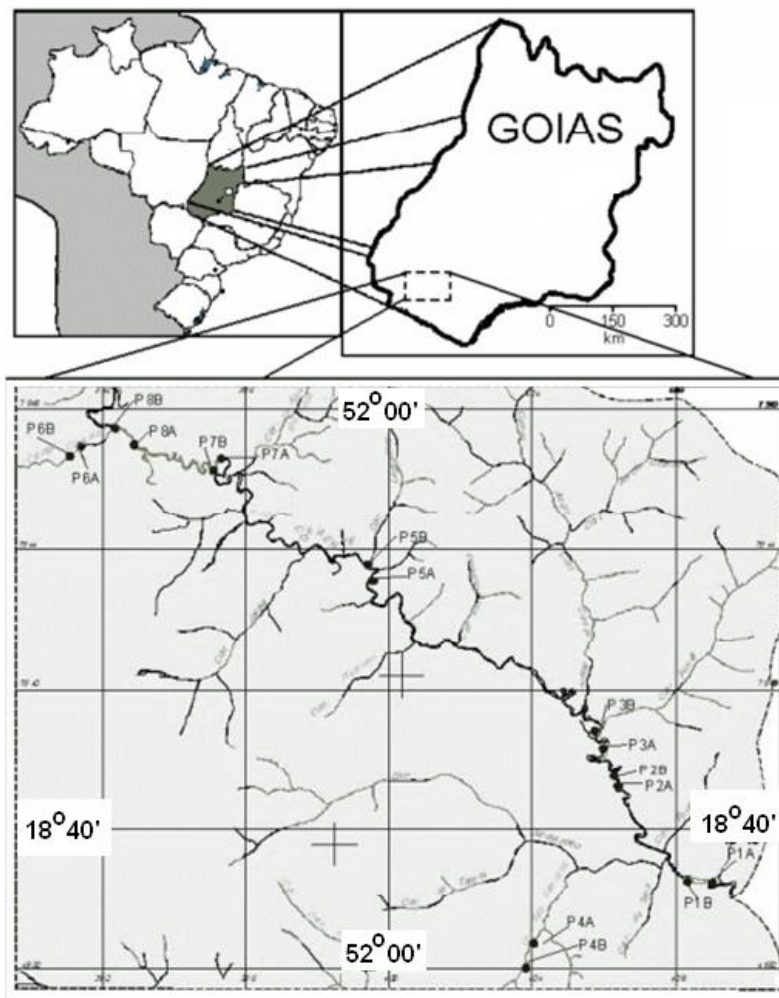


Figure 1. Map of the region with localization of Corrente River and sampling areas (Goiás State – Brazil)

Ecopath Model. Ecopath software (Christensen & Walters 2004) was the tool used to construct the food web model for the Corrente River. Ecopath combines estimative to biomass and consumption of various elements in an aquatic ecosystem (Polovina, 1984) based on the theory for analysis of flows among elements of an ecosystem (Ulanowicz 1986). A basic requirement in these models is the mass balance which assumes that input to each group should be equal to output (i.e. steady state conditions). To accomplish this assumption, a series of biomass budget equations to each biological compartment was performed based on the following procedure:

Production – all predation on each grouping
 – non-predatory mortality – all exports = 0

The resulting budget equations were transformed into simultaneous equations according to the formula:

$$0 = B_i * PB_i * EE_i - \sum_{ij} (B_j * QB_j * DC_{ji}) - EX_i \quad (2)$$

The parameter B_i represents the biomass of i while PB_i is the production/biomass ratio of i that is equal to natural mortality rate (M) given that there is not fishing activity at the study site. EE_i correspond to ecotrophic efficiency, i.e. the fraction of the production of i that it is consumed within the system or is exported. B_j is the biomass of predators, QB_j represents food consumption per unit of biomass for consumer j and DC_{ji} is the fraction of the prey i in the diet of the predator j . Lastly EX_i is the exported biomass of i and as data for this parameter were not available, EX_i was assumed as zero for all species.

Each fish species was represented by one compartment and represented by parameters assessed to each taxon. Empirical regressions were used to estimate QB (Palomares & Pauly, 1998) and PB (Pauly, 1980). For PB estimation data from scientific literature was also used (Angelini & Agostinho, 2005a) while B was assessed by virtual population analysis (VPA) in Fisat (Sparre *et al.* 1989, FAO-ICLARM 1996). If B values were not

available, it was used EE values between 0.8 and 0.99, since these values are frequent in a reasonable number of Ecopath models (Christensen 1995, Angelini & Gomes 2008). After EE values input, Ecopath was able to estimate biomass (B).

A pedigree index was calculated through Ecopath to quantify the uncertainty related to the input values in the model (Christensen *et al.* 2005). Ecopath estimates mean of pedigree values associated to each input value, resulting in an overall pedigree index ranging from 0 (low precision information) to 1 (data and parameters fully rooted in local data). For each input value (B, PB, QB, DC) the quality and confidence of the data were described concerning to high or low precision and the source of data (sample-based information, from other models or literature).

The Ecoranger routine was used to test model sensitivity, assess its viability and find a better model when less accurate data are available (Christensen & Pauly 1992). This routine reduces possible technical errors since it adjusts input parameters accordingly based on normal distribution with mean equal to each input value and interval confidence defined by user (Villanueva *et al.* 2006a). Procedures assumed for other compartments that comprise the Ecopath model are described below.

Phytoplankton. The plankton net (20 μm) was used and sampling was active for 15 minutes. Phytoplankton density was estimated according to APHA (1998) and individuals $\times \text{mm}^3$ unit (CTE 2005) was converted to biomass using biovolume ($\text{mm}^3 \times \text{litro}^{-1}$) and multiplied by 2 m (euphotic zone) and then $\text{ton} \times \text{km}^{-2}$ (Total river area = 3 km^2). PB value ($300 \times \text{yr}^{-1}$) was assumed according to literature (see Angelini & Agostinho 2005b).

Zooplankton. The plankton nets (63 $\square\text{m}$) were used conjointly to water pump to filter 500 L water per sample. Individuals were counted in Sedwigck-Rafter camera using a microscope and were weighed with results in $\text{mgr} \times \text{m}^{-3}$ transformed to $\text{ton} \times \text{km}^{-2}$ (same as the phytoplankton). PB ($55.0 \times \text{yr}^{-1}$) and QB ($250.0 \times \text{yr}^{-1}$) values as well as diet composition were based on models in the literature (Angelini & Petrere 1996, Angelini & Agostinho 2005b).

Aquatic Macrophytes. The biomass value for this group ($388.17 \text{ t} \times \text{km}^{-2}$) was taken from aquatic macrophytes monitoring report data (CTE 1999), with biomass samples in $\text{gr} \times \text{m}^{-2}$ for the more abundant species while PB value ($10 \times \text{yr}^{-1}$) was taken from the literature (Angelini & Agostinho 2005b).

Terrestrial Invertebrates. Despite this

group of organisms have been not sampled at the study site, it proved to be an important item in the diet of some species. For this reason, values for PB ($30.0 \times \text{yr}^{-1}$), QB ($250 \times \text{yr}^{-1}$), EE (0.8) and diet composition were gathered from the literature (Angelini *et al.* 2006, Angelini & Agostinho 2005b).

Ecopath outputs. Ecopath software estimates some ecosystem attributes including those concerning to system aging and stability (*sensu* Odum 1969) such as Total Primary Production divided by Total Respiration (Pp/R) which is expected to be near unity in mature ecosystems and higher than those in systems in early phases of development, because in such case the system needs to accumulate biomass, i.e., needs to increase production.

Total Primary Production divided by Biomass (Pp/B; excluding detritus) is also estimated by Ecopath and it is expected to be higher in immature systems as well as Finn cycling index, which represents the proportion from overall flows recycled in a system and according to theory will be higher in more mature systems indicating higher recycling and recovery capacity (Vasconcellos *et al.* 1997). Likewise, the number of energy paths (Path number) in the food web and the mean length of paths (Path length) are important indicators of redundancy in a system given that more paths greater connectivity and resilience and lengthy paths imply in higher energy flow potential through the system until top predators, showing better use of the energy in the system (Christensen 1995).

However, stability, redundancy and consequently maturity are better determined by goal functions such as ascendancy – A and overhead – O (Ulanowicz 1986). Overhead is positively correlated with maturity and stability (Christensen 1995) and when added to A it supplies the System Development Capacity, i.e., the total quantity of information a system has for its own development.

The mixed trophic impact matrix adapted from economics was also constructed. This matrix estimates trophic impact from an increase in biomass of a single compartment on the other compartments, including any direct path (predator or prey) or indirect among these groups (Christensen *et al.* 2005). Ecopath supplies the information regarding to the changes caused by the impacting group (negative: diminishes biomass or positive: increase biomass) and makes possible understand if the impacting group has a top-down or bottom-up control on the impacted group.

KS_i index (Libralato *et al.* 2006) which is based on the mixed impact trophic matrix was used in order to identify key species in the food web and

to its control on the system (top-down or bottom-up).

$$KS_i = \log[\varepsilon_i (1 - p_i)] \quad (3)$$

Where:

KS_i = keystone index

ε_i = root of $\sum mij^2$, where mij is mixed trophic impact matrix value, i.e., negative or positive impact from one group on the others, so ε_i is the measure of the relative overall effect of each group on the food web in which the effect of the change in biomass on the group itself (i.e., mii) is not included.

p_i = B_i / Total B, where B_i – biomass of impacting group divided by total biomass (excluding detritus)

This index has the property of attributing high values of keystone to functional groups that

have both low biomass proportions and high overall effects (Libralato *et al.* 2006). It also provides a full description of the species by splitting the negative and positive contributions of impacted groups (mij) from the overall effect, and supplies the information regarding to bottom-up and top-down effects of the species. Accordingly the relative contribution (%neg) of negative values of mij (top-down control) must be separated from the positives ones (bottom-up control).

Results

Composition and structure of the fish assembly. A total of 1140 individuals belonging to 4 families (1 subfamily) and 7 species were collected. *Astyanax altiparanae* was the most abundant specie and richness was alike for all habitats in exception to *Hypostomus strigaticeps* which was not sampled in lentic areas (Table I).

Table I. Species of fish sampled from the Corrente River (GO) during the study period (2003-2005).

Family/SubFamily Species	Popular name	Abundance (N)		
		Main channel	Tributaries	Lentic areas
Characidae				
<i>Astyanax altiparanae</i>	Lambari	293	157	80
<i>Astyanax fasciatus</i>	Lambari	38	34	4
<i>Brycon nattereri</i>	Pirapitinga	72	66	2
<i>Salminus hilarii</i>	Tubarana	51	5	16
Anostomidae				
<i>Leporinus friderici</i>	Piau-três-pintas	81	3	10
Loricariidae/Hypostominae				
<i>Hypostomus strigaticeps</i>	Cascudo	1	11	-
Erythrinidae				
<i>Hoplias malabaricus</i>	Traíra	119	13	84
Individuals Total		655	289	196

Morisita similarity index was higher between the river and tributaries environment ($C_H=0.91$), but was also high between the main channel and lentic area ($C_H=0.88$), as well as between the tributaries and lentic area ($C_H=0.70$).

Reproductive activity was registered to all habitats at a low rate at the first sample months and markedly intense during the rainy season (September to December; Table II).

Table II. Reproductive activity for fish species in Corrente River (GO) between June 2003 and June 2005 (N: number of specimens analyzed; P: proportion of individuals in reproductive activity; highest values in bold).

Specie	March		May		June		September		December	
	N	P (%)	N	P (%)	N	P (%)	N	P (%)	N	P (%)
<i>S. hilarii</i>	11	0	28	0	3	0	2	0	16	68
<i>A. altiparanae</i>	63	8	79	0	108	1,6	42	93	149	20
<i>A. fasciatus</i>	9	6	22	13	9	0	2	25	24	76
<i>B. nattereri</i>	37	4	32	47	15	66	11	9	31	6
<i>L. friderici</i>	21	4	27	0	13	0	5	60	20	33
<i>H. malabaricus</i>	32	5	58	1	38	0	14	21	60	15

Feeding Index (IAi) was determined by the analysis of 102 gut contents indicating

that two species have carnivorous habit (*S. hilarii* and *H. malabaricus*) while the others showed a trend to an omnivore diet (Table III).

Table III. Proportion of resources used by each species given by feeding index $-IA_i$ (oma: organic animal matter; sca: fish scale; ins: insect; inv: other invertebrates; fruits: refers to fruits and seeds; veg: vegetation; deb: debris/sediment).

Species	Itens								
	oma	sca	ins	inv	fruits	algae	veg	deb	fish
<i>S. hilarii</i>	1.45		2.50						96.05
<i>A. altiparanae</i>		0.002	85.00	0.004	2.994	2.00	10.00		
<i>A. fasciatus</i>	27.67	3.02	19.18	0.0001	0.0059	0.12	50.00	0.004	
<i>B. nattereri</i>		0.1	74.21		21.86		3.55	0.28	
<i>L. friderici</i>	0.16	0.1	63.36		5.59	0.47	29.63	0.69	
<i>H. malabaricus</i>		0.004	36.086		0.05	0.17	0.17	0.52	63.00

Since all habitats were similar in species composition and richness and that as gut contents as reproductive activity were identical at all habitats it was reasonable and suitable to build a single trophic model for the entire

section of the Corrente River under study, as showed below.

Ecopath model. Data from Table III produced the diet composition matrix (Table IV) to elaborate the Ecopath model.

Table IV. Diet composition of the compartments of model for Ecopath for Corrente River (2004-2005). Predators are in columns and preys in lines.

Prey \ Predator	3	4	5	6	7	8	9	10	11
1 Phytoplankton	0.4		0.001	0.02		0.004			
2 Macrophytes		0.2	0.5	0.1	0.036	0.1		0.007	
3 Zooplankton									
4 Terrestrial Invertebrates			0.192	0.85	0.742	0.634		0.361	0.025
5 <i>Astyanax fasciatus</i>								0.1	0.06
6 <i>Astyanax altiparanae</i>								0.5	0.74
7 <i>Brycon nattereri</i>									0.115
8 <i>Leporinus friderici</i>									0.05
9 <i>Hypostomus strigaticeps</i>									0.01
10 <i>Hoplias malabaricus</i>								0.03	
11 <i>Salminus hilarii</i>									
12 Detritus Animal			0.307	0.0006	0.001	0.01		0.001	
13 Detritus	0.6	0.3			0.003		1	0.001	
14 Import		0.5		0.029	0.219	0.252			
SUM	1	1	1	1	1	1	1	1	1

From the two detritus compartments in the model, Animal Detritus get all mortality and excretion from components 4 to 11 (Table IV) since *A. fasciatus* and *B. nattereri* are consumers of organic animal matter and fish scales (Table III), but they are not piscivorous. Diet of *H. malabaricus* and *S. hilarii* in Corrente system relied mainly upon *A. altiparanae*.

Table V shows input values for Corrente model and some estimated values for biomass (B) and ecotrophic efficiency (EE) run by Ecopath.

Pedigree index estimated was 0.7 indicating high reliability for input data since the index varies

from 0 (not reliable) to 1. Model also showed good fit since from 496 runs of Ecoranger routine, 200 were acceptable and the least sum of deviation was low (0.252). The initial inputs and outputs based on our field data were very close to the mean values generated by Ecoranger.

In exception to value of Total Primary Production divided by Total Respiration (Pp/R = 1.55), according to the parameters outputs Corrente River was an immaturity system with undeveloped food web (Total Primary Production divided by Biomass - Pp/B = 33.7; Finn cycling index = 0.01%; Overhead - O = 36.3%; Path number = 63 and mean length path = 2.96).

Table V. Inputs and outputs (in parentheses) for basic parameters from Ecopath of Corrente River (B - biomass; PB - production/biomass; QB - consumption/biomass; EE - ecotrophic efficiency from Eq. (2); TL - trophic level estimated by Ecopath).

Biological group	TL	B (t/km ²)	P/B (/year)	Q/B (/year)	EE
Phytoplankton	1	2.621	250	-	(0.96)
Macrophytes	1	38	27	-	(0.04)
Zooplanckton	2	6.29	50	250	(0.0)
Terrestrial Invertebrates	2	(0.745)	30	250	0.8
<i>Astyanax fasciatus</i>	2.19	0.22	3	14.3	(0.481)
<i>Astyanax altiparanae</i>	2.88	1.175	3	14.6	(0.587)
<i>Brycon nattereri</i>	2.95	(0.218)	0.72	8.4	0.8
<i>Leporinus friderici</i>	2.85	(0.0832)	0.82	7.5	0.8
<i>Hypostomus strigaticeps</i>	2	0.05	1.09	27.4	(0.2)
<i>Hoplias malabaricus</i>	3.49	0.3	0.93	8.4	(0.271)
<i>Salminus hilarii</i>	3.81	(0.12)	0.41	9.1	0
Detritus Animal	1	-	-	-	(0.001)
Detritus	1	-	-	-	(0.99)

Leontief matrix and keystone rank.

The mixed trophic impact matrix (Fig. 2) indicates that very small fraction of changes in biomass of *S. hilarii* would have negative effects upon *Brycon nattereri*, *L. friderici* and *H. strigaticeps*.

Similarly small changes in *A. altiparanae* biomass would have negative impact upon those species mentioned above and in addition on terrestrial invertebrates whereas it would have positive effect upon macrophytes.

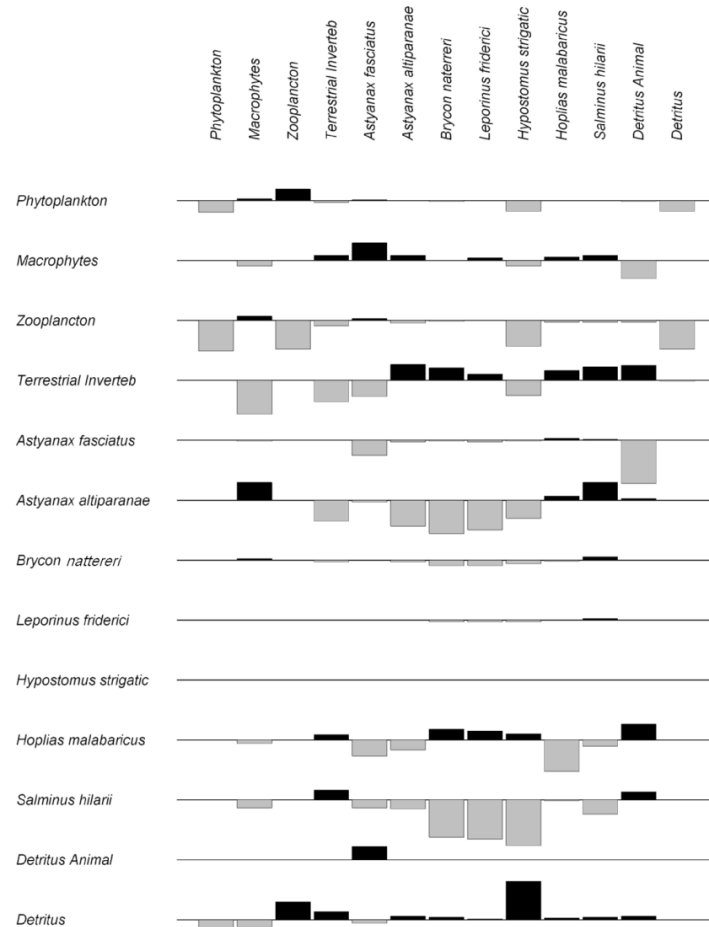


Figure 2. Mixed trophic impact matrix of the Ecopath Model for Corrente River (Brazil). Bars up indicating a positive effect on group of the columns caused by respective group in line (bars down, negative effect).

The keystone rank values (Fig. 3) placed *S. hylarii* (KSi= 0.10; TL = 3.81) as top predator followed by *A. altiparanae* (KSi = -0.016; TL = 2.88; intermediate trophic level) beyond two compartments of trophic level 2: terrestrial invertebrates (KSi = -0.064;

TL = 2.0) and zooplankton (KSi = -0.13 TL = 2.0; Fig. 3). Terrestrial invertebrates compartment is influenced by allochthonous material because half of its diet items are imported (Table IV), that is, it depends on the vegetation along the river.

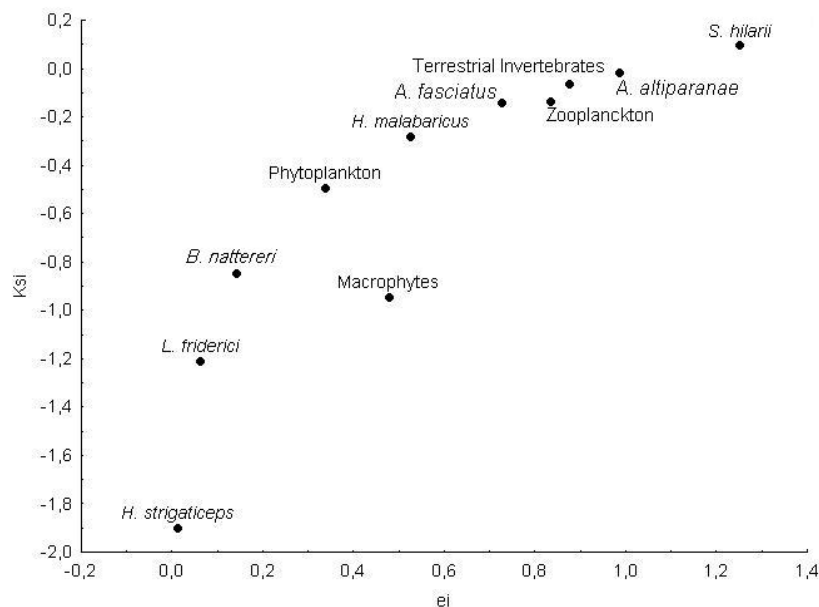


Figure 3. Keystone index (KSi) for the groups in the Corrente model. For each group KSi (y axis) is reported against overall effect – ei (x axis). Groups are ordered by decreasing keystone index.

Discussion

As in any Ecopath model structured in Brazil, main uncertainties for data input in Corrente model were related to fish biomass estimates since fish species were sampled by gill nets which are gears quite selective to fish size, displacement in water column and are ineffective to catch visual predator species. The lack of sampled information regarding to terrestrial invertebrate in the model was also a constraint since this group was important for diet composition to some fish species (*A. altiparanae*, *B. nattereri* and *L. friderici*).

Nonetheless since data were to a large extent based on direct observations, pedigree index (0.7) assured model's reliability given that indexes varying from 0.16 to 0.68 are truly reliable (Pedersen *et al.* 2008). Further, Corrente model is strongly fitted as runs in Ecoranger routine provided values which have no prominent dissimilarity from original input, showing which model is consistent (Villanueva *et al.* 2006b).

Nevertheless comparisons of Corrente model results with other systems are restricted, because it is usual modeling by Ecopath huge rivers with large floodplains (Angelini & Agostinho 2005a,

Angelini *et al.* 2006) instead of small rivers, such as Corrente with few compartments generated by low richness and abundance. However these environments, in Brazil, have been increasingly utilized for power generation purposes through the installation of Small Hydroelectric Units. This lack of studies has been a constraint to any further and future understanding regarding to the impacts from hydroelectric generation. Since 2007, the Espora Hydroelectric project (32MW) was installed in Corrente River and currently two additional projects are under legal dispute since Espora dam has crashed at January 2008. For this reason, data presented here have ecological and economical interest and could be the only source of information to subsidize future evaluation for the Corrente River under hydroelectric effects.

Fish community in Corrente River was homogeneous since: i) all of the species were captured in all habitats (exception to *H. strigaticeps*); ii) all similarity values among habitat were high, indicating relative agreement among species abundances; iii) all species reproduce in all the environments during the rainy season, exception to *B. nattereri*, which reproduces during the dry

season; iii) regardless of species' high feeding plasticity, there is low seasonal variability in the gut content, although many authors consider diet seasonality common and related to the variable availability of allochthonous material (Araújo-Lima *et al.* 1995, Melo *et al.* 2004).

Evenness in Corrente River's fish community seems has been influenced by physical features given that borders for the three types of environment studied herein were formed by small and degraded riparian woods or pastures and farmland. The influence of this type of vegetation in the fish community has already been well established (Cetra & Petrere 2007, Sarmento-Soares *et al.* 2009) and it may be one of the factors for the reduced richness. Additionally, the high hydrodynamic energy and waterfalls in the studied section must have obstructed the arrival of migrating species from upstream Paranaíba River, since there is no record of migrating species in the studied stretch. This scenario of species occurrence, reproduction and feeding preference allowed that one single Ecopath model could be carried out.

The equality of Corrente River habitats coupled to its running flow homogenizes the environment and it inhibits, for example, high primary production and influences ecosystem attribute values modeled like Pp/R and Pp/B. Regardless, this ecosystem tends to make few use of recycled material in the system as showed by low Finn index, resulting in lower overhead. For that reason the system has less resilience partly due to the few number of energy paths (only 63) which stems from low local richness (7 species and just 11 compartments in the model) resulting in tiny connectance (redundancy) and consequently few stability. This implies in slight ecosystem ability in recover from severe changes such as dams construction and turns the outcomes to food web unsure.

Trophic models frequently describe systems processes as top-down or bottom-up (Forrester *et al.* 1999, McIntosh *et al.* 2005) and discuss factors such as land-water ecotone and vegetation along the rivers as the forces controlling food web processes (Wallace *et al.* 1997, Nystrom *et al.* 2003).

Despite keystone rank values do not express directly the type of food web control, it has been recently used to infer how the food web's system operates (Libralato *et al.* 2006) and in a system with just 11 compartments, the trophic levels of the first four key species seem able to reveal how food web operates. It implies that in Corrente River the food web control is mixed ever since piscivorous *S. hilarii* and "terrestrial invertebrates" have a large

impact upon food web and both operate together on the Corrente River trophic web. Also *A. altiparanae*, the most abundant species, is an important prey for the piscivorous and a predator on "Terrestrial Invertebrates" highlighting the interaction of top down and bottom up control on Corrente River food web and supporting a mixed control on the system.

Mixed control differs from top-down or bottom-up food web aforementioned and from wasp-waist control which takes place when just species of intermediary trophic level strongly influences the entire food web (Hunt & McKinnel 2006).

Food web control is an important feature of ecological communities that may be strongly influenced by disturbance like damming, especially in ecosystems with low richness such as Corrente River. Shifts in trophic structure can alter stability and affect richness and modify total biomass. Our assessment provides an overview of river's characteristics and demonstrates its poor stability. This would imply that species replacement and changes in food web control mechanisms resulting from disturbance are both unpredictable. We suggest that ecosystems attributes play an important role in ecosystems assessment and should be additional information to understand ecosystem structure and functioning.

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