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Food web model of the Upper Paraná River Floodplain: description and aggregation effects

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Abstract

To describe the Upper Paraná River Floodplain (the last non-dammed stretch of the Paraná River, Brazil) a food web model was quantified using ECOPATH. The modeled ecosystem showed maturity because of the total primary production/total respiration ratio (close to 2), Finn's cycling index (7%) and overhead (65%). The first model elaborated had 40 compartments/groups, but its transfer efficiencies among trophic levels did not reduce in despite the trophic level increasing. To solve this, the effect of two grouping methods on system-level information and other ecosystem attributes was investigated. The first series tested, named "classic" (researcher intuitive way and by food preferences) also did not reduce transfer efficiencies. In the second series, named "by pathways", the first species grouping were those with higher number of input pathways and longest mean length of pathways. Thereby, the news groups from aggregation decreased the number of components and system's richness, but stability (measured by overhead) did not change, including the model with only eight compartments. The great number of the ten compartments that showed these characteristics was piscivores, increasing the redundancy within highest trophic level. The use of pathways (number and length) can be useful to lumping species since it reduces compartments and do compromise neither maturity nor stability, diminishing grouping subjectivity.
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1. Introduction

In the history of ecological research, documenting "what eats what" has been a priority and the most obvious interaction is the predation that sometimes controls herbivory, and is responsible for the length

of food chains (Hairston et al., 1960; Schoener, 1989; Hall and Raffaelli, 1993; Paiva et al., 1994).

Food webs described in mathematical models can be useful in multi-specifics management decision (Vasconcellos et al., 1997; Christensen and Pauly, 1998; Wolff et al., 2000; Moreau et al., 2001; Bundy and Pauly, 2001), in analyses of effects of the trophic cascade (Polis et al., 2000; Ortiz and Wolff, 2002; Schmitz et al., 2004) and to verify the relationship among stability and diversity (Hastings, 1988; Naeem and Li, 1997; Tilman, 1999).

Food webs are synonymous of ecosystems. Lindeman (1942) and Odum (1969) established the description of ecosystem development (succession) restrict by 2^a thermodynamic law. This last author showed how to measure the development phase of ecosystems (or food webs), that determines theirs resilience (stability).

Ecosystems or food webs are quantified in compartments models where the practice of grouping species is a common exercise. This aggregation is made frequently among species with similar diet, diminishing the system complexity and facilitating its comprehension (Hakanson, 1995; Martinez, 1991). Aggregation is sometimes a convenient tool to study complex system with hierarchical structure (Auger et al., 2000).

Aggregation implies however in a series of problems: aggregation can convey in uncertain on parameters values and incorrectness conclusions. Abarca-Arenas and Ulanowicz (2002) show that the way of aggregation can significantly affect the value of ascendency, a measure of stability originating from the information theory (Ulanowicz, 1996, 1997).

The aim of this work are: (i) to quantify the ecotrophic community of the Upper Paraná River Floodplain and (ii) to study the effect of two grouping methods of species on system-level information and other ecosystem attributes.

2. Methods

2.1. Study area

The Paraná River is formed by the junction of the Grande and Paranaíba Rivers in south-central Brazil, and flows into the La Plata River in northern Argentina (Fig. 1). It is the tenth longest river in the world

(4,695 km), and has a 2.8 km $\times$ 10^6 km drainage area that includes most of the south-central part of South America (18–34°S; 45–68°W). The Upper Paraná River includes approximately the first third of the Paraná River Basin, and is whole in Brazilian territory, except for a stretch within Itaipu Reservoir that borders with Paraguay. In the eastern margin (Grande, Paranaíba, Tietê, and Paranapanema rivers) there are 130 major reservoirs (dam > 10 m height), among these 20% are larger than 10,000 ha, and four are located in the Paraná River main channel with area ranging from 48,200 to 151,300 ha (Gomes and Miranda, 2001).

The Upper Paraná River floodplain is the last non-dammed stretch of the Paraná River with an extensive alluvial plain and great accumulation of sediments giving rise to more than 300 islands (Agostinho and Zalewski, 1995). In spite of upstream dammings, the flood regime is the principal factor that acts on the communities of area (Thomaz, 1991).

2.2. The Ecopath model

For the purpose of our study will be used the Ecopath model, originally proposed by Polovina (1984a) and further developed by Christensen and Pauly (1993a). It is a mass-balance description of trophic interactions. The foundations of Ecopath are the theories of Odum (1969) and Ulanowicz (1997) and so, it is possible to describe systems in terms of their development (maturity) and resilience.

The basic condition considered for Ecopath model is that input to each group is equal to the output from it (equilibrium conditions). Then, a series of biomass budget equations are determined for each group as:

Production − all predation on each grouped species − non-predatory mortality − all exports = 0 which can be re-expressed as:

$$0 = B_i \times PB_i \times EE_i - \sum_j (B_j \times QB_j \times DC_{ji}) - EX_i \tag{1}$$

where B_i is the biomass of the group (i); (PB_i) is the production/biomass ratio, usually assumed equal to the total mortality (Z_i); EE_i is the ecotrophic efficiency, i.e. the proportion of the ecological production which is consumed by predators or exported and usually assumed to range from 0.7 to 0.99 (Polovina, 1984b); B_j
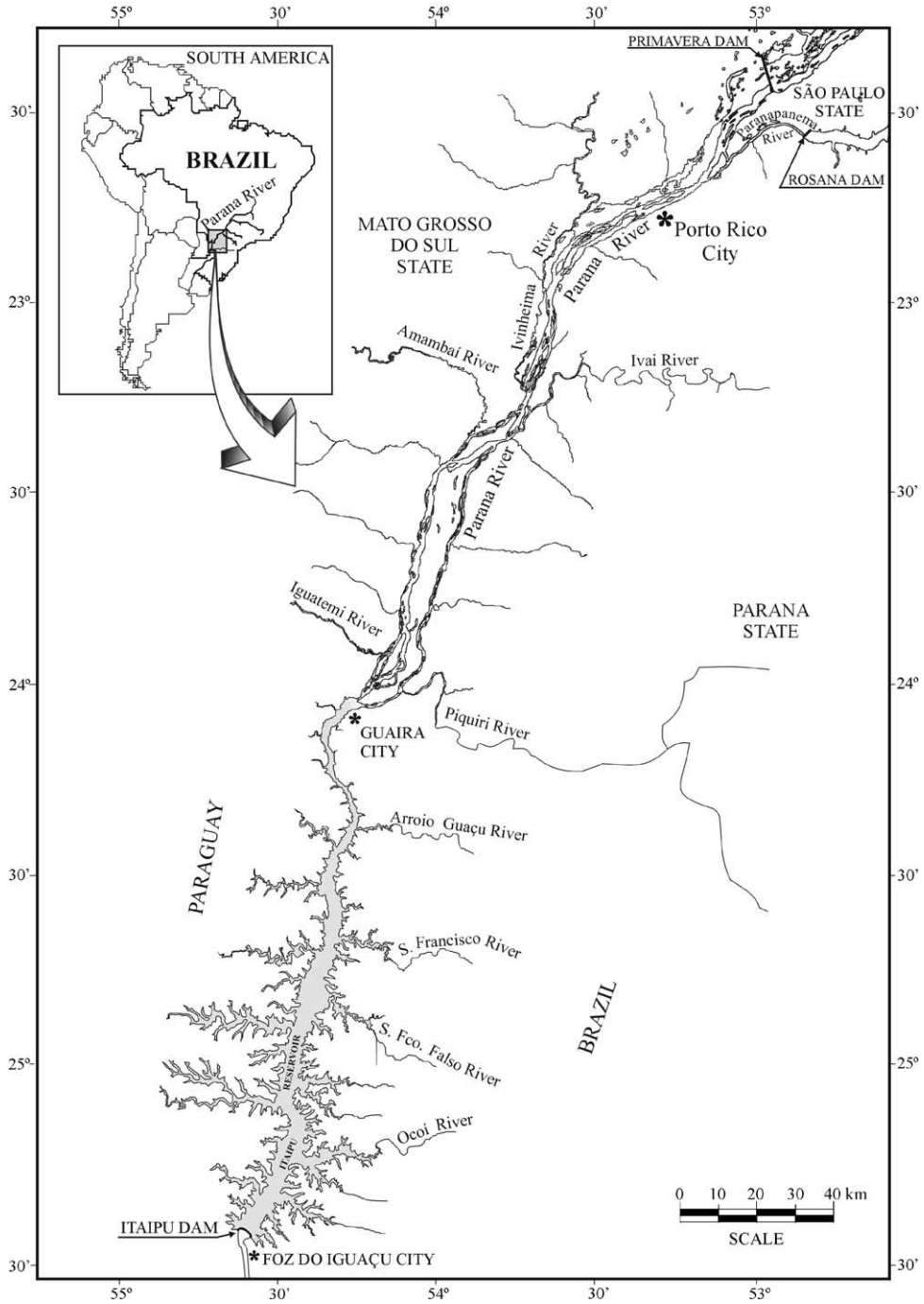
Fig. 1. Map of the region with localization of Upper Paraná River Floodplain.

the biomass of predator (j); QB_j is the food consumption per unit of biomass for predator j and DC_{ji} is the fraction of i in the diet of j; EX_i is the export of (i).

Therefore, a system with n groups (boxes) will have n linear equations. Since Ecopath links the different groups, it allows the estimation of one unknown parameter for each group. The data required for Ecopath were assembled and standardized to ton $\times$ km^{-2} and ton $\times$ km^{-2} $\times$ year^{-1}.

2.3. Data source

Table 1 shows the references used for input concerning the "non-fish" compartments of the Planície model.

Sampling of fish was conducted at each three months on the various habitats (river, channels, lakes), from March 1992 to February 1995. It was used gill nets (2–16 cm mesh) and trammel nets (6–8 cm mesh). Fishing gears were deployed for 24 h sampling periods, with inspections at early morning, dusk and late evening. Fishes were anesthetized with tricaine or oil of cloves before being sorted by species, counted and measured.

2.4. Selection of fish's compartments

Each of the 28 fish species more abundant was represented by one compartment (components 7–34 in Table 2), for which PB was calculated using Z (total mortality), QB using Palomares and Pauly (1998) and B was assessed by Ecopath or in some cases by virtual population analysis (VPA) in Fisat (FAO-ICLARM, 1996; Sparre et al., 1989; Angelini and Agostinho, submitted for publication). When required, i.e., when B was unknown, EE's values were provided all between 0.9 and 0.99.

Five others fish compartments were assembled to the model (components 35–39 in Table 2) resulting from grouping 143 other species accenting to their diet composition. For those species PB and QB, were calculated as an average of compartments with same trophic level.

Diet composition was quoted mainly in Hahn et al. (1997) and Agostinho et al. (1997), but also other sources were used: Almeida et al. (1997) to piscivores; Andrian and Barbieri (1996) to *Parauchenipterus galeatus*; Ferreti et al. (1996) to *Schizodon* spp.; Lolis and Andrian (1996) to *Pimelodus maculatus*; Andrian et al. (1994) to *Leporinus* spp.; Souza-Stevaux et al. (1994) to *Pterodoras granulosus*; Marques (1993) to *Pseudoplatystoma corruscans*; Fugi (1993) and Fugi and Hahn (1991) to benthos and detritus feeders; Hahn et al. (1992, 1991) to *Pterodoras granulosus* and *Trachydoras paraguayensis*, respectively.

2.5. Grouping species

The effect of grouping species on system-level information and other attributes was investigated by two ways of aggregation of a 40-compartment model of Upper Paraná River Floodplain, called original and used as a control. From this model two series of aggregated variations were produced.

The first series is the "classic" one and assumes the role of a researcher, whom normally would lump species in an intuitive way and by food preferences.

The second series is "by pathway". In this attempt, the first species groupings were those with higher number of input pathways and longest mean length of pathways. Input pathways refer to number of pathways leading to one specific group (or compartment) and mean path length is defined as total number of groups that an inflow passes through before leading to one

Table 1

Sources of the "non-fishes" data used to compile the trophic network for the Upper Paraná River floodplain model

Compartment	Reference
Phytoplankton	B in Ecopath; PB in Train and Rodrigues, 1997; Thomaz (1991) and Thomaz et al. (1997); EE in Silva Jr. (1998)
Aquatic macrophytes	B in Thomaz and Bini (1999); PB in Cook (1990)
Periphyton	B and PB in Rodrigues (1998)
Benthos	B in Takeda et al. (1997); PB in Brey (1999) and Morin and Bourassa (1992); diet composition and QB in Mihuc (1997) and Cummins and Klug (1979)
Zooplankton	B in Ecopath; PB in Angelini et al. (1996); diet composition in Lansac-Tôha et al. (1997); QB in Sipaúba-Tavares et al. (1994); EE in Silva Jr. (1998)
Insects	B in Ecopath; PB, QB, EE and diet composition in Silva Jr. (1998)

Table 2
Basic parameters inputs and outputs (in parentheses) from Ecopath of the PLANÍCIE (1992–1995)

	Compartment	B	PB	QB	EE	Trophic level	No. of pathways	Pathways length
1	Phytoplankton	(0.063)	250.00	–	0.90	1		
2	Aquatic macrophytes	35.00	10.00	–	(0.11)	1		
3	Periphyton	7.40	20.00	–	(0.66)	1		
4	Benthos	4.80	10.40	40.00	(0.10)	2	(2)	(1)
5	Insects	(0.60)	25.00	250.00	0.70	2	(2)	(1)
6	Zooplankton	(0.08)	55.00	250.00	0.70	2	(2)	(1)
7	*Hypostomus* spp.	0.001	2.46	25.00	(0.64)	2	(2)	(1)
8	*P. maculatus*	(0.004)	1.99	14.84	0.99	3.1	(1032)	(6.49)
9	*Schizodon borelii*	(0.003)	3.47	25.00	0.99	2	(2)	(1)
10	*Loricariichthys platymetopon*	(0.0001)	4.12	42.00	0.99	2.3	(6)	(1.67)
11	*Prochilodus lineatus*	(0.051)	4.56	47.00	0.99	2.2	(4)	(1.5)
12	*Cyphocharax modesta*	(0.001)	3.32	33.80	0.99	2.1	(4)	(1.5)
13	*Steindachnerina insculpta*	(0.001)	4.77	48.00	0.99	2.1	(4)	(1.5)
14	*Iheringichthys labrosus*	0.005	2.27	19.27	(0.83)	2.7	(8)	(1.75)
15	*Schizodon altoparanae*	(0.0001)	1.83	26.22	0.99	2	(2)	(1)
16	*Hypophthalmus edentatus*	0.04	1.85	20.87	(0.79)	2.7	(3)	(1.67)
17	*Trachydoras paraguayensis*	(0.003)	2.42	17.00	0.99	2.5	(5)	(1.8)
18	*Hoplosternum littorale*	0.006	4.13	29.00	(0.84)	2.6	(8)	(1.75)
19	*Leporinus friderici*	(0.021)	2.42	18.97	0.99	2.6	(51)	(3.18)
20	*Leporinus obtusidens*	0.34	2.85	30.00	(0.98)	2.6	(34)	(2.68)
21	*Parauchenipterus galeatus*	(0.031)	2.90	26.20	0.99	2.6	(3)	(1.67)
22	*Pterodoras granulosus*	0.06	1.04	16.05	(0.93)	2.3	(9)	(1.67)
23	*Astyanax altiparanae*	(0.446)	3.00	21.00	0.99	2.7	(34)	(2.68)
24	*Auchenipterus nuchalis*	0.016	2.71	20.00	(0.73)	3.1	(13)	(2.46)
25	*Brycon orbignyanus*	(0.015)	0.92	5.87	0.99	2.8	(76)	(3.99)
26	*Acestrorhyncus lacustris*	0.006	2.22	7.80	(0.88)	3.6	(116)	(3.63)
27	*Hoplias malabaricus*	(0.002)	2.67	9.00	0.99	3.8	(202)	(4.3)
28	*Plagioscion squamosissimus*	0.09	1.13	5.21	0.73	3.7	(1032)	(6.6)
29	*Pseudoplatystoma corruscans*	(0.007)	2.82	10.0	0.99	4	(1698)	(6.22)
30	*Rhaphiodon vulpinus*	0.01	1.40	10.0	(0.72)	3.8	(242)	(4.47)
31	*Serrasalmus marginatus*	(0.048)	2.00	7.21	0.99	3.8	(1032)	(6.02)
32	*Hemisorubin platyrhynchos*	0.006	1.30	5.37	(0.89)	3.8	(1767)	(6.83)
33	*Salminus brasiliensis*	(0.002)	1.00	3.71	0.99	3.6	(260)	(4.83)
34	*Serrasalmus spilopleura*	(0.030)	1.60	6.73	0.99	3.8	(1032)	(7.43)
35	Other benthos feeders	(0.025)	3.90	29.0	0.99	2.6	(9)	(1.67)
36	Other detritus feeders	(0.015)	4.30	43.0	0.99	2.2	(6)	(1.67)
37	Other insectivores	(0.025)	3.90	27.0	0.99	2.9	(39)	(3.43)
38	Other piscivores	(0.003)	4.00	15.0	0.99	3.7	(1698)	(6.85)
39	Other omnivores	(0.414)	5.00	33.0	0.99	2.6	(10)	(1.60)
40	Detritus	–	–	–	0.21	1	–	–

B, biomass; PB, production/biomass; QB, consumption/biomass; EE, ecotrophic efficiency (Eq. (1)). Flux in (ton $\times$ km^2 $\times$ year^{-1}) and biomass in (ton $\times$ km^2).

specific compartment/number of input pathways of the specific compartment (Finn, 1980; Christensen, 1995).

An important attribute used to compare those two grouping methods was transfer efficiency calculated as the ratio of the flow that is transferred from one discrete trophic level to the next and the throughput at the discrete trophic level (Christensen and Pauly, 1993b).

3. Results

The diet matrix is given in Table 3. Table 2 summarizes the so-called ORIGINAL Ecopath model and shows the number of input pathways and mean length of pathways of each compartment. Surprisingly in this balanced model, the transfer efficiencies from Lindeman

Table 3

Diet composition of the compartments of PLANICIE model for Ecopath in the Upper Paraná River Floodplain (1992–1995)

	Prey/predator	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Phytoplankton			0.5	0.2	0.05	0.3	0.1	0.15	0.35	0.35		0.3	0.3			0.05	0.05		0.1
2	Macrophytes		0.3			0.05	0.7						0.7			0.1	0.3	0.3	0.4	0.5
3	Periphyton	0.5										0.1								
4	Benthos					0.25		0.1	0.15	0.1	0.1	0.35				0.2	0.05	0.05		0.1
5	Insects					0.1		0.2				0.2			0.15	0.2	0.2	0.2	0.6	0.1
6	Zooplanckton					0.1						0.1		0.7	0.3	0.2				0.1
7	*Hypostomus* spp.																			
8	*P. maculatus*																			
9	*S. borelii*																			
10	*L. platymetopon*																			
11	*P. lineatus*																			
12	*C. modesta*																			
13	*S. insculpta*																			
14	*I. labrosus*																			
15	*S. altoparanae*																			
16	*H. edentatus*																			
17	*T. paraguayensis*					0.1														
18	*H. littorale*																			
19	*L. friderici*					0.05														
20	*L. obtusidens*																			
21	*P. galeatus*																			
22	*P. granulosus*																			
23	*A. altiparanae*					0.1											0.1	0.1		
24	*A. nuchalis*																			
25	*B. orbignyanus*																			
26	*A. lacustris*																			
27	*H. malabaricus*																			
28	*P. squamosissimus*																			
29	*P. corruscans*																			
30	*R. vulpinus*																			
31	*S. marginatus*					0.05														
32	*H. platyrhynchos*																			
33	*S. brasiliensis*																			
34	*S. spilopleura*																			
35	Other benthos feeders																			
36	Other detritus feeders																			
37	Other insectivores					0.05														
38	Other piscivores																			
39	Other omnivores																0.1	0.1		
40	Detritus	0.5	0.7	0.5	0.8	0.1		0.6	0.7	0.55	0.55	0.25			0.55	0.3	0.2	0.2		0.1

	Prey/predator	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
1	Phytoplankton	0.1												0.05	0.1			0.1
2	Macrophytes	0.2		0.3										0.1		0.2		0.15
3	Periphyton																	0.1
4	Benthos													0.35	0.1			0.15
5	Insects	0.3	0.7	0.55										0.1	0.1	0.6		0.3
6	Zooplanckton	0.1	0.2											0.1		0.1		0.1
7	*Hypostomus* spp.											0.2						
8	*P. maculatus*										0.25							
9	*S. borelii*				0.1												0.1	
10	*L. platymetopon*											0.15						
11	*P. lineatus*					0.2	0.3		0.2	0.1		0.15	0.1				0.2	
12	*C. modesta*				0.1													
13	*S. insculpta*										0.2							
14	*I. labrosus*				0.2													
15	*S. altoparanae*											0.1						
16	*H. edentatus*									0.1			0.1				0.1	
17	*T. paraguayensis*																	
18	*H. littorale*							0.3										
19	*L. friderici*						0.1											
20	*L. obtusidens*	0.1				0.2		0.1										
21	*P. galeatus*						0.15		0.2									
22	*P. granulosus*					0.2				0.1			0.1					
23	*A. altiparanae*			0.1	0.2	0.15	0.2	0.2	0.1	0.15	0.1	0.1				0.1	0.2	

Table 3 (*Continued*)

	Prey/predator	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
24	*A. nuchalis*				0.1			0.1					0.1					
25	*B. orbignyanus*									0.1		0.1						
26	*A. lacustris*					0.1		0.1										
27	*H. malabaricus*					0.2						0.2						
28	*P. squamosissimus*									0.1			0.2					
29	*P. corruscans*									0.05							0.05	
30	*R. vulpinus*								0.1									
31	*S. marginatus*						0.1	0.1		0.1	0.1							
32	*H. platyrhynchos*							0.1										
33	*S. brasiliensis*																0.05	
34	*S. spilopleura*					0.1												
35	Other benthos feeders		0.1						0.1	0.1			0.1					
36	Other detritus feeders				0.1					0.1	0.1		0.1					
37	Other insectivores			0.05	0.1	0.1	0.1			0.1	0.1							
38	Other piscivores							0.1									0.1	
39	Other omnivores	0.1			0.1					0.05		0.1	0.1				0.2	
40	Detritus	0.1												0.3	0.7			0.1

The sum of colums is 1.

pyramid did not present lower values in higher trophic levels (original model in Table 4).

Therefore, an aggregation or removal of compartments by the "classical" way (researcher experience and food preferences) was attempted. Nevertheless, the anterior atypical structures remained, in exception of model with eight compartments (see Table 4).

In other way the compartments with the most number of input pathways and longest ones were lumping (Table 2). Fig. 2 presents the relationship between the number of input pathways and mean length of pathways for the ORIGINAL model of Upper Paraná River floodplain.

Whereupon the initials grouping on the ORIGINAL model were (Fig. 2):

- GI: *P. maculatus*, *P. squamosissimus*, *S. marginatus* and *S. spilopleura*;
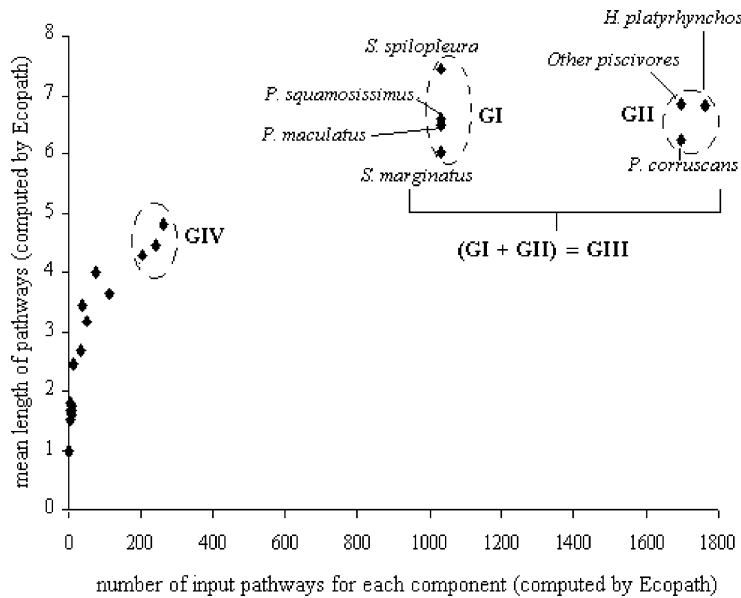- GII: *P. corruscans*, *H. platyrhynchos* and "other piscivores";

Fig. 2. Relationship between mean length of pathways and number of input pathways for each compartment (both computed by Ecopath, see values in Table 2). GI, GII, GIII and GIV are groups to adjust the transfer efficiency between trophic levels (see text and Table 4).

Table 4
Transfer efficiency between trophic levels for PLANÍCIE model (values in %)

Way to group compartments	No. of compartments	Trophic level								Clusters (numbers of components, see Table 2)
		II	III	IV	V	VI	VII	VIII	IX	
		Transfer efficiency								
Original	40	4.9	9.2	4.3	8.5	11.2	12.7	12.8	15.0	See Table 2
By pathways	35	4.9	10.5	5.5	7.6	10.2	5.9	3.3	2.7	GI = 8+ 28+ 31 + 34; GII = 29 + 32 + 38
By pathways	34	5.1	10.7	6.9	10.1	11.1	4.4	2.4	–	GIII = GI + GII
By pathways	32	5.1	10.5	6.1	6.6	3.7	2.0	0.0	–	GIII; GIV = 27 + 30 + 33
By pathways	28	4.9	9.7	5.5	7.0	3.7	2.2	0.0	–	GIII; GIV; GV= 37 + 25 + 19; G6 = 20 + 23 + 24
By pathways	25	5.0	9.7	5.6	6.8	3.7	2.2	0.0	–	GIII; GIV; GV; GVI; GVII = 22 + 35 + 39; GVIII = 14 + 18
By pathways	19	5.0	9.7	5.6	6.9	3.7	2.2	0.0		GIII;GIV;GV;GVI;GVII;GVIII; GIX = 10 + 36; GX = 11 + 12 + 13; GXI = 16 + 21; GXII = 7 + 9 + 15
By pathways	17	5.0	9.5	4.2	4.2	1.9	0.0			GIII; GV; GVI; GVII; GIX; GX; GXI; GXII; GXIII = GVIII + 17; GXIV = GIV + 26
By pathways	13	5.1	8.7	3.9	2.4	0.0				GXV = GV + GVI; GXVI = GVII + GXIII; GXVII = GIX + GX; GXVIII = GXI + GXII
By pathways	8	6.1	5.8	1.5	0.0					GXIX = 1 + 2 + 3; GXX = 4 + 5 + 6; GXXI = GIII + GXIV; GXVIII; GXVII; GXVI; GXV; Detritus
Original	40	4.9	9.2	4.3	8.5	11.2	12.7	12.8	15.0	See Table 2
Classic	35	9.0	12.9	15.9	17.4	21.2	20.6	20.2	20.3	Free 35, 36, 37, 38, 39
Classic	32	8.2	13.1	18.4	18.6	20.8	21.3	20.6	22.4	Free bigger migratory species: 11, 22, 20, 25, 29, 30, 32, 33
Classic	27	9.2	14.3	17.5	17.3	19.4	19.1	18.5	17.2	Grouping: 9 + 15; 11+ 12 + 13; 19 + 20; 27 + 28; 29 + 30; 31 + 34; and remainder components
Classic	22	5.4	11.3	7.4	7.1	5.2	2.8	4.9		Grouping: 7 + 10; 8 + 21; 9 + 15 + 16; 11 + 12 + 13; 14 + 17 + 18; 19 + 20 + 22; 23 + 24 + 25; 26 + 27 + 30; 29 + 32 + 33; 31 + 34; and remainder components
Classic	17	9.9	12.0	18.2	19.3	17.4	20.1	20.9	20.8	Same like a prior, but free 35, 36, 37, 38, 39
Classic	14	9.7	11.3	20.7	21.0	22.3	21.4	20.1	19	Grouping: 7 + 10 + 11 + 12 + 13; 8 + 21; 9 + 15 + 16; 14 + 17 + 18; 19 + 20 + 22; 23 + 24 + 25; and remainder components
Classic	8	6.3	5.9	1.8	0.0					Grouping: 1 + 2+ 3; 4 + 5 + 6; 26 + 27 + 28 + 29 + 30 + 31 + 32 + 33 + 34; 7 + 10 + 11 + 12 + 13 + 14; 8 + 19 + 20 + 21 + 22; 9 + 15 + 16; 17 + 18 + 23 + 24 + 25; 40

Ways to group species: (a) By pathways – initializing with components with higher number of pathways and pathways length (Table 2) (b) Classic – researcher's knowledge ("intuition") referring to similarities in diet.

- GII: GI + GII;
- GIV: *H. malabaricus*, *R. vulpinus* e *S. brasiliensis*.

These compartments have the higher number of pathways (1032–1767) and the longest ones (6.02–7.43).

This aggregation method ("by pathways") caused an efficiency decrease (Table 4) and did not alter other ecosystems attributes (Fig. 3), like overhead and ascendency (Fig. 3a). Development capacity was altered only in model with eight components (Fig. 3b).

Fig. 3c and 3d show respectively two attributes by Odum (1969) to evaluate the development stage of ecosystems: (i) total primary production/total respira-

tion, close to 1 in mature ecosystems. In PLANÍCIE, this attribute is near of 2, indicating high maturity or just to stand out a low primary production; and (ii) Finn cycling index to indicate recycling matter in the system. In PLANÍCIE, this attribute is the same during the aggregation and its value is close to many other ecosystems (Christensen and Pauly, 1993c).

4. Discussion

Christensen (1994, 1995) evaluated 41 ecosystems with Ecopath and asserted that from seven main attributes, sole two showed good correlation with
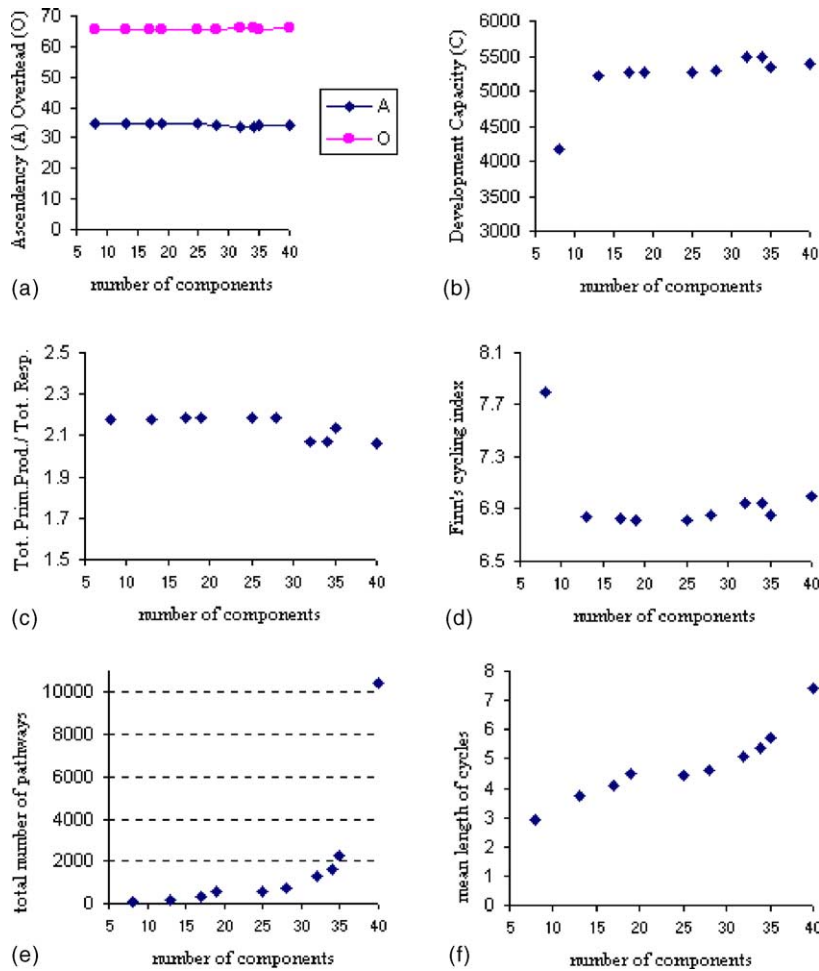
Fig. 3. Behavior of some ecosystems attributes in the aggregation of groups/compartments by pathway (number and length): (a) overhead and ascendency; (b) development capacity; (c) TPP/TR; (d) Finn index; (e) number of pathways; (f) length of pathways.

maturity: pathways number (flux diversity) and the mean length of the pathways. The use of both to grouping components, maintained the maturity of PLANÍCIE (Fig. 3a and c), although those attributes have been drastically reduced (Fig. 3e and f).

In the first moment, number and length of pathways would be inconsistent with increase of transfer efficiencies, because lengthening food chain diminishes efficiency. Although since Lindeman (1942), it is known that predators are more generalists than their preys. In PLANÍCIE, predation among piscivores generates feeding loops, originating great redundancy in the higher trophic levels and maintaining the transfer efficiencies elevated (Table 4). High richness of top predators also contributed for transfer efficiencies did not decrease in the Terminos Laguna in the Mexico Gulf (Manickchand-Heileman et al., 1998).

Hence, it is clear that predation on other trophic levels is very important for the piscivores, but an observation from these results is that high redundancy within an upper trophic level diminished it dependence on lower level, whereas predation among piscivores can apparently sustain their own biomass.

Aggregation performed by pathway (number and length), reduced the intraguild predation and diminished transfer efficiencies, however stability was maintained high. Naeem and Li (1997) showed that more species by functional group (in this case, the groupings), assert the existence of communities more consistent in biomass and density.

Solow and Beet (1998) concluded that stability in groups is higher than in isolate populations and describe that higher redundancy in diet, facilitate aggregation in observed trophic webs.

However, Paiva et al. (1994) showed that increase in predator abundance diminish the fishery and the system biologic production. Top predators and aggressive invaders (in our case, *P. squamossissimus* and *S. marginatus*) may have richly spreading effects through their feeding links, and therefore playing role in community organization by indirect effects. Fulton et al. (2003) agree that predation is a crucial part of ecosystem models.

The Upper Paraná River floodplain has many microhabitats (river, channels, lagoons), increasing local diversity and allowing an intricate food web with many pathways (Hahn et al., 1997). This high system redundancy collaborates with stability (overhead), maturity (total primary production/total respiration) and with the flux internalization that help the ecosystem development (Christensen and Pauly, 1998). However, PLANÍCIE maturity do not provide higher biomass because the high number of predatory species. These results agree with Takimoto et al. (2002), which suggest that temporal productivity differences between spatially linked habitats are important to promote the stability of food web dynamics in a landscape context.

Comparisons with PLANÍCIE model are very limited, because there is no previous floodplain model in Ecopath. Weber et al. (1996) and Lopes et al. (2004), for instance, emphasized in theirs floodplain simulation models other subjects, which are not appropriately comparable with PLANÍCIE. Nevertheless, attributes values from PLANÍCIE are very close with other aquatic ecosystem modeled utilizing the Ecopath (Christensen and Pauly, 1993c): ratio total primary production/total respiration was close to 2, Finn's cycling index was near by 7% and overhead 65%.

5. Conclusion

Abarca-Arenas and Ulanowicz (2002) showed that the effects of species clustering affect not just the final values of goal functions, but also the global structure of trophic network. The use of pathway (number and length) for species lumping can be useful since reducing the number of compartments, does not compromise stability and diminishes grouping subjectivism.

Although Power et al. (1995) affirmed that to understand food web dynamics on floodplain rivers, heterogeneity in both space and time needs to be taken into account, we believe that the average pattern described in PLANÍCIE model is suitable during the whole year.

PLANÍCIE model permits interdisciplinary research, despite generalizations that diminish precision and realism. This preliminary approach could connect investigations in different compartments and to introduce hypothesis that might be studied more thoroughly (by Ecospace) and systematically (by Ecosim) in the future, increasing the importance of the integrity's maintenance of this segment of Paraná River, which should be necessarily linked to a greater rationalization for the operation of the dams upstream.

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References

Abarca-Arenas, L.G., Ulanowicz, R.E., 2002. The effects of taxonomic aggregation on network analysis. Ecol. Model. 149, 285–296.

Agostinho, A.A., Hahn, N.S., Gomes, L.C., Bini, L.M., 1997. Estrutura trófica. In: Vazzoler, A.E.M., Agostinho, A.A., Hahn, N.S. (Eds.), A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e sócio-econômicos. Ed da Universidade Estadual de Maringá, PR, Brazil, pp. 229–248.

Agostinho, A.A., Zalewski, M., 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Paraná River, Brazil. Hydrobiologia 303, 141–148.

Almeida, V.L.L., Hahn, N.S., Vazzoler, A.E.A.M., 1997. Feeding patterns in five predatory fishes of the high Paraná River floodplain (Brazil). Ecol. Freshwater Fish 6, 123–133.

Andrian, I.F., Barbieri, G., 1996. Revista Brasileira de Biologia. Espectro alimentar e variações sazonal e espacial na composição da dieta de Parauchenipterus galeatus LINNAEUS, 1766, (SILURIFORMES AUCHENIPTERIDAE) na região do Reservatório de Itaipu (PR) 56 (2), 409–422.

Andrian, I.F., Doria, C.C.R.C., Torrente, G., Ferreti, C.M.L., 1994. Espectro alimentar e similaridade na composição da dieta de 4 espécies de Leporinus (Characiformes, Anostomidae) do Rio Paraná, Brasil. Revista UNIMAR 16 (3), 97–106.

Angelini, R., Agostinho, A.A., submitted for publication. Parameters Estimates for Fishes of the Upper Paraná River Floodplain and Itaipu Reservoir (Brazil). NAGA The WorldFishe Center.

Angelini, R., Abuabara, M.A.P., Rietzler, A.C., 1996. Application of de Bernardi and Di Cola model in a Argyrodiaptomus furcatus (zooplankton – copepod) from Broa Reservoir (São Carlos SP-Brazil). Memorie dell'Istituto Italiano di Idrobiologia 54, 69–75.

Auger, P., Charles, S., Viala, M., Poggiale, J.-C., 2000. Aggregation and emergence in ecological modeling: integration of ecological levels. Ecol. Model. 127, 11–20.

Brey, T., 1999. A collection of empirical relations for use in ecological modelling. Naga, The ICLARM Quarterly 22 (3), 24–28.

Bundy, A., Pauly, D., 2001. Selective harvesting by small-scale fisheries: ecosystem analysis of San Miguel Bay, Philippines. Fish. Res. 53, 263–281.

Christensen, V., 1995. Ecosystem maturity – towards quantification. Ecol. Model. 77, 3–32.

Christensen, V., 1994. On the behavior of some proposed goal functions for ecosystem development. Ecol. Model. 75/76, 37–49.

Christensen, V., Pauly, D., 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecol. Appl. 8 (1), S104–S109.

Christensen, V., Pauly, D. (Eds.), 1993a. Trophic models of aquatic ecosystems. ICLARM, Manila, The Philippines, p. 390.

Christensen, V., Pauly, D., 1993b. On steady-state modelling of ecosystems. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, The Philippines, pp. 14–19.

Christensen, V., Pauly, D., 1993c. Flow characteristics of aquatic ecosystems. In: Christensen, V., Pauly, D. (Eds.), Trophic Models of Aquatic Ecosystems. ICLARM, Manila, The Philippines, pp. 338–355.

Cook, C.D.K., 1990. Origin, autoecology, and spread of some of the world's most troublesome aquatic weeds. In: Pieterse, A.H., Murphy, K.J. (Eds.), Aquatic Weeds: The Ecology and Management of Nuisance Aquatic Vegetation. Oxford Science Publications, New York, pp. 31–38.

Cummins, K.W., Klug, M.J., 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10, 147–172.

FAO-ICLARM, 1996. Stock Assessment Tools. User's Manual. Ed: FAO-ICLARM, Roma, 123 pp.

Ferreti, C.M.L., Andrian, I.F., Torrente, G., 1996. Dieta de duas espécies de Schizodon (CHARACIFORMES, ANOSTOMIDAE), na planície de inundação do alto rio Paraná e sua relação com aspectos morfológicos. Boletim do Instituto de Pesca 23, 171–186.

Finn, J.T., 1980. Flow analysis of models of the Hubbard Brook ecosystem. Ecology 6, 562–571.

Fugi, R., Hahn, N.S., 1991. Espectro alimentar e relações morfológicas com o aparelho digestivo de 3 espécies de peixes comedoras de fundo do Rio Paraná. Revista Brasileira de Biologia 51 (4), 873–879.

Fugi, R., Estratégias alimentares utilizadas por cinco espécies de peixes comedores de fundo do alto rio Paraná: Dissertação de Mestrado em Ecologia e Recursos Naturais, Universidade Federal de São Carlos, 1993, p. 142.

Fulton, E.A., Smith, A.D.M., Johnson, C.R., 2003. Mortality and predation in ecosystem models: is it important how these are expressed? Ecol. Model. 169, 157–178.

Gomes, L.C., Miranda, L.E., 2001. Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the Upper Paraná River. Regulat. Rivers: Res. Manage. 17, 67–76.

Hahn, N.S., Andrian, I.F., Fugi, R., Almeida, V.L.L., 1997. Ecologia trófica. In: Vazzoler, A.E.M., Agostinho, A.A., Hahn, N.S. (Eds.), A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e sócio-econômicos. Ed. da Universidade Estadual de Maringá, Maringá/PR, pp. 209–228.

Hahn, N.S., Monfredinho, A., Fugi, R., Agostinho, A.A., 1992. Aspectos da alimentação do armado, Pterodoras granulosus (OSTARIOPHYSI DORADIDAE) em distintos ambientes do Alto Rio Paraná. Revista UNIMAR 14, 163–176.

Hahn, N.S., Fugi, R., Andrian, I.F., 1991. Espectro e atividade alimentares do armadinho, Trachydoras paraguayensis (Doradidae Siluriformes) em distintos ambientes do Rio Paraná. Revista UNIMAR 13 (2), 177–194.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. Am. Naturalist 94, 421–425.

Hakanson, L., 1995. Optimal size of predictive models. Ecol. Model. 78, 195–204.

Hall, S.J., Raffaelli, D.G., 1993. Food webs: theory and reality. Adv. Ecol. Res. 24, 187–239.

Hastings, A., 1988. Food web theory and stability. Ecology 69 (6), 1665–1668.

Lansac-Tôha, F.A., Bonecker, C.C., Velho, L.F.M., Lima, A.F., 1997. Composição, distribuição e abundância da comunidade zooplanctônica. In: Vazzoler, A.E.M., Agostinho, A.A., Hahn, N.S. (Eds.), A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e sócio-econômicos. Ed. da Universidade Estadual de Maringá, pp. 117–155.

Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. Ecology 23, 399–418.

Lolis, A.A., Andrian, I.F., 1996. Alimentação de *Pimelodus maculatus* Lacépede, 1803 (Siluriformes, Pimelodidae) na planície de inundação do alto rio Paraná Brasil. Boletim do instituto de pesca 23, 187–202.

Lopes, L.F.G., Do Carmo, J.S.A., Cortes, R.M.V., Oliveira, D., 2004. Hydrodynamics and water quality modelling in a regulated river segment: application on the instream flow definition. Ecol. Model. 173, 197–218.

Manickchand-Heileman, S., Arreguín-Sánchez, F., Lara-Domínguez, A., Soto, L.A., 1998. Energy flows and network analysis of Terminos Lagoon, SW Gulf of Mexico. J. Fish. Biol. 53 (A), 179–197.

Marques, E.E., 1993. Biologia reprodutiva, alimentação natural e dinâmica de nutrição do pintado, Pseudoplatystoma corruscans (Agassiz, 1829) (Osteichtyes Pimelodidae) no alto rio Paraná: Dissertação de Mestrado em Ciências Biológicas. Universidade Federal do Paranás.

Martinez, N.D., 1991. Artifacts or attributes? Effects of resolution on the little rock Lake Food Web. Ecol. Monogr. 61 (4), 367–392.

Mihuc, T.B., 1997. The functional trophic role of lotic primary consumers: generalist versus specialist strategies. Freshwater Biol. 37, 455–462.

Moreau, J., Villanueva, M.C., Amarasinghe, U.S., Schiemer, F., 2001. Trophic relationships and possible evolution of the production under various fisheries management strategies in a Sri Lanka reservoir. In: De Silva, S.S. (Ed.), Reservoir and Culture-Based Fisheries: Biology and Management (Canberra), pp. 201–214.

Morin, A., Bourassa, N., 1992. Modules empiriques de la production annuelle et du rapport P/B d'invertebras benthiques d'eau courante. Can. J. Fish. Aquat. Sci. 49, 532–539.

Naeem, S., Li, S., 1997. Biodiversity enhances ecosystem reliability. Nature 390, 507–509.

Odum, E.P., 1969. The strategy of ecosystem development. Science 104, 262–270.

Ortiz, M., Wolff, M., 2002. Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios. Ecol. Model. 148, 277–291.

Paiva, M.P., Petrere, M., Petenate, A.J., Nepomuceno, F.H., Vasconcelos, E.A., 1994. Relationship between the number of predatory fish species and fish yield in large North-eastern Brazilian reservoirs. In: Cowx, I.G. (Ed.), Rehabilitation of Freshwater Fisheries. Fishing New Books, pp. 120–129.

Polis, G.A., Sears, A.L.W., Huxel, G.R., Strong, D.R., Maron, J., 2000. When is a trophic cascade a trophic cascade? Trends Ecol. Evol. 15, 473–475.

Polovina, J.J., 1984a. An overview of the Ecopath model. Fishbyte 2 (2), 5–7.

Polovina, J.J., 1984b. Model of a coral ref. ecosystem I: the Ecopath model and its application to French Frigate Shoals. Coral Reefs 3 (1), 1–11.

Power, M.E., Parker, G., Dietrich, W.E., Sun, A., 1995. How does floodplain width affect floodplain river ecology? A preliminary exploration using simulations. Geomorphology 13, 301–317.

Rodrigues, L., 1998. Sucessão do perifíton na Planície de Inundação do Alto Rio Paraná: Interação entre nível hidrológico e regime hidrodinâmico. Tese de doutorado. Ecologia de Ambientes Aquáticos Continentais. Universidade Estadual de Maringá (Maringá PR), 175 p.

Schoener, T.W., 1989. Food webs from small to the large. Ecology 70 (6), 1559–1589.

Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecol. Lett. 7, 153–163.

Silva Jr, U.L., 1998. Análise da produção pesqueira de um lago de várzea do Baixo Amazonas através de um modelo de balanço de massas. Dissertação de mestrado. Instituto Nacional de Pesquisas da Amazônia, Manaus (AM).

Sipaúba-Tavares, L.H., Bachion, M.A., Rocha, O., 1994. Estudo do crescimento populacional de três espécies zooplanctônicas em laboratório e o uso do plâncton na alimentação de alevinos de Oerochromis niloticus (tilápia) e Astyanax scabripinis paranae (lambari). Rev. UNIMAR 16 (Suplemento 3), 189–201.

Solow, A.R., Beet, A.R., 1998. On lumping species in food webs. Ecology 79 (6), 2013–2018.

Souza–Stevaux, M.C., Negrelle, R.R.B., Citadini-Zanette, V., 1994. Seed dispersal by the fish *Pterodoras granulosus* in the Paraná River Basin Brazil. J. Trop. Ecol. 10, 621–626, short communication.

Sparre, P., Ursin, E., Venema, S.C., 1989. Introduction to tropical fish stock assessment. Part 1. Manual. FAO, Fisheries Technical Paper, Rome, 337 p.

Takeda, A.Y., Shimizu, G.Y., Higuti, J., 1997. Variações espaço–temporais da comunidade zoobêntica. In: Vazzoler, A.E.M., Agostinho, A.A., Hahn, N.S. (Eds.), A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e sócio-econômicos. Ed. da Universidade Estadual de Maringá, pp. 157–177.

Takimoto, G., Iwata, T., Murakami, M., 2002. Seasonal subsidy stabilizes food web dynamics: balance in a heterogeneous landscape. Ecol. Res. 17, 433–439.

Thomaz, S.M., 1991. Influência do regime hidrológico (pulsos) sobre algumas variáveis limnológicas de diferentes ambientes aquáticos da planície de inundação do alto rio Paraná (MS–Brasil). Dissertação de Mestrado: Universidade Federal de São Carlos, p. 293.

Thomaz, S.M., Bini, L.M., 1999. A expansão das macrófitas aquáticas e implicações para o manejo de reservatórios: um estudo da represa de Itaipu. In: Henry, R. (Ed.), Ecologia de Reservatórios: Estrutura, Função e Aspectos Sociais. Ed Fapesp e Fundibio, pp. 597–626.

Thomaz, S.M., Roberto, M.C., Bini, L.M., 1997. Caracterização limnológica dos ambientes aquáticos e influência dos níveis fluviométricos. In: Vazzoler, A.E.M., Agostinho, A.A., Hahn, N.S. (Eds.), A Planície de Inundação do Alto rio Paraná: Aspectos Físicos, Biológicos e Sócio-econômicos. Ed. da Universidade Estadual de Maringá, pp. 73–102.

Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80 (5), 1455–1474.

Train, S., Rodrigues, L.C., 1997. Distribuição espaço - temporal da comunidade fitoplanctônica. In: Vazzoler, A.E.M., Agostinho, A.A., Hahn, N.S. (Eds.), A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e sócio-econômicos.

Editora da Universidade Estadual de Maringá, pp. 105–115.

Ulanowicz, R.E., 1997. Ecology, the Ascendent Perspective. Columbia University Press, p. 201.

Ulanowicz, R.E., 1996. Trophic flow networks as indicators of ecosystem stress. In: Polys, A.G., Winemiller, K.O. (Eds.), Food Webs. Integration of Patterns and Dynamics. Chapman and Hall, pp. 358–368.

Vasconcellos, M., Mackinson, S., Sloman, K., Pauly, D., 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecol. Model. 100, 125–134.

Weber, G.E., Furch, K., Junk, W.J., 1996. A simple modelling approach towards hydrochemical seasonality of major cations in a Central Amazonian floodplain lake. Ecol. Model. 91, 39–56.

Wolff, M., Koch, V., Isaac, V., 2000. A trophic model of Caeté Mangrove Estuary (North Brazil) with considerations for the sustainable use of its resources. Estuarine, Coastal Shelf Sci. 50, 789–803.