Trophic models in Neotropical reservoirs: Testing hypotheses on the relationship between aging and maturity

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ABSTRACT

Damming of rivers is one of the main human interferences in natural ecosystems. With the purpose to analyze food webs in 30 reservoirs of the state of Paraná, southern Brazil, we built standardized models (same number of compartments) for each reservoir in the software Ecopath. We tested the existence of an association among eight attributes described in Odum's theory (estimated by the models built in Ecopath and summarized in a Principal Component Analysis—PCA) and some characteristics of the reservoirs, such as age and area. Compartments were categorized in two groups: 'non-fish' (phytoplankton, periphyton, rotifers, copepods, cladocerans, bacteria, protozoans, benthos and detritus) and 'fish' (omnivorous, insectivorous, piscivorous, herbivorous, detritivorous and invertivorous). To balance the models, diet (main food items) and biomass of some groups (especially periphyton) were modified to get values of ecotrophic efficiency lower than one. We found that Axis 1 of the PCA (which represented 37.1% of the variability of the original data matrix) was significantly correlated with three categories from Odum's theory: community energetics, homeostasis and structure. Axis 2 (20.2%) was not correlated with the attributes, whereas axis 3 (15.6%) was significantly correlated with nutrient cycling and life history. Reservoir age was negatively correlated with axis 1; hence, older reservoirs seemed to be more developed (or senesced) than younger ones. Thus, it is possible to conclude that maturity (or senescence) is an inherent characteristic of reservoir aging, regardless of human interference, reservoir area or number of species. Therefore, the results presented here are additional evidence of the importance to improve Odum's central theory of ecosystem development. In spite of some limitations, we believe that the Ecopath model applied to these reservoirs is a feasible tool for interdisciplinary environmental studies.

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1. Introduction

Damming has been one of the main human interferences in natural ecosystems in the past 5000 years. The main purposes of dam building are flood control, irrigation, water supply, aquaculture and generation of electricity (Tundisi and Matsumura-Tundisi, 2003; Nilsson et al., 2005; Olías et al., 2011). The reservoirs formed are frequently viewed as unstable ecosystems, because they are mixed systems that have features of the original river (lotic) and features of the new lentic condition, such as decomposition of submerged vegetation, higher water retention time, stratification, higher depth (Tundisi, 1990), eutrophication and changes in fish assemblage composition; species with pre-adaptations

to lentic conditions and invasive fish are favored (Gomes and Miranda, 2001a; Agostinho et al., 2008; Johnson et al., 2008; Kahn and Panikkar, 2009). Several uses of reservoirs also alter the trophic status of the ecosystem (Agostinho et al., 1999; Villanueva et al., 2006a; Hoeinghaus et al., 2008) as well as independent variables, such as rainfall, winds, age, latitude and presence of tributaries.

The artificial conditions that result from damming cause habitat changes with severe consequences for species richness, abundance and foraging of fish assemblages (Agostinho et al., 2004; Nilsson et al., 2005; Miranda and Hunt, 2011). In addition, changes in food availability cause a large restructuration of the food web, which results in a new ecosystem structure (Baxter, 1977). Food web structure and interactions, which are subjects of several ecological studies, play a major role in determining the dynamics of an ecosystem (Kitchell et al., 2000; Aoki and Mizushima, 2001; Angelini and Agostinho, 2005a; Gamito and Erzini, 2005).

To analyze those features and the new food web formed due to damming, an ecosystem approach is needed, because this approach gives important insights to support fish stock assessment and has potential to improve the knowledge about the process of development in ecosystems (Walters et al., 1997; Mace, 2001; Hilborn et al., 2003; Link, 2010; Nielsen and Ulanowicz, 2011). Thus, the ecosystem approach can provide the basis for testing several scenarios of usage and can serve as base for examining the ecological potential to increase biological production, since damming modify the local biodiversity and affect ecosystem services (Angelini et al., 2006; Agostinho et al., 2007; Hoeinghaus et al., 2009).

The modern ecosystem approach was proposed by Lindeman (1942) and Odum (1969), who modeled ecosystem development (succession) taking into account restrictions imposed by the second law of thermodynamics. Odum (1969) defined 24 ecosystem attributes aiming at describing their development and at understanding ecosystem resilience through time. As a general rule, Odum's theory assumes that mature systems would be more resilient, because they have higher species richness and, consequently, higher number of trophic interactions, which would be dependent on detritus recycling to sustain larger biomass/total flow rates. These features would result in lower net production, since total respiration should maintain high biomass.

Nowadays, the ecosystem theory deals mostly with elucidation of thermodynamic implications of macroscale ecosystem processes (Jørgensen and Fath, 2004; Ulanowicz et al., 2009) and has been improved by approaches which, in general, disengaging ecosystem growth or increase in the size of a system, from ecosystem development, that is an internal reorganization of energy mass stores and their transferences (Fath et al., 2004) over time, changing from immaturity to senescence (Salthe, 2002).

These ideas and their metrics are useful to detect patterns in ecosystems (for instance, distinct stages of development) and to test the performance of each component of an ecosystem. Some of those patterns were detected when Christensen (1995) compared maturity among 41 aquatic ecosystems using 31 attributes calculated in the software Ecopath (Christensen and Pauly, 1992). He established ecosystem goal functions (optimization functions) based on a maturity ranking, and found a high correlation between maturity and overhead, an emergent propriety proposed by Ulanowicz (1986) that measures the disorder of a system. This property is the opposite of ascendency, which measures order in a system. Nonetheless, results from Christensen (1995) and Christensen and Pauly (1998) studies on ecosystem maturity, despite confirming key principles of Odum's theory, could not be related to aging. It is impossible to determine the age of natural environments in a suitable scale required by the ecosystem approach.

Reservoirs are unique environments: as they are man-made, their exact age can be determined. Therefore, they are suitable systems to test hypotheses on the relationship between aging and maturity. In the present study, we used the software Ecopath to model 30 reservoirs located in the State of Paraná, southern Brazil. We aimed at testing for an association between the attributes described in Odum's theory (estimated by models built in Ecopath) and some characteristics of the reservoirs. First, we described possible trends in eight attributes that summarize ecosystem bioenergetics (Total Primary Production/Total Respiration, Net Production Ecosystem and Abundance), community structure (Species Richness), life history (Total Biomass/Total Production), recycling and homeostasis (Finn Cycling Index, System Development Capacity and Schrödinger Ratio). Then, we related these attributes to reservoir surface area, age and other features. We hypothesized that resilience is an inherent characteristic of reservoir aging, regardless of human interference or area, i.e., older reservoirs are

more resilient, what does not mean that they have more biomass or production.

2. Materials and methods

2.1. The reservoirs

The 30 studied reservoirs were located in six river basins in the State of Paraná (Brazil): Paranapanema River (seven reservoirs), Tibagi River (three), Iguaçu River (twelve), Ivaí River (two), Piquiri River (two) and Leste basin (four reservoirs; Fig. 1). Climate in all reservoirs is the same: dry winter and rainy summer. They have different uses, such as water supply, recreation and generation of electricity; the latter is the main purpose of all reservoirs. Like the other reservoirs in South America, fishery productivity in these reservoirs is low (Petrere Jr., 1996; Okada et al., 1997), and fishing intensity is very low. Reservoir selection was based on a wide range of age, size, water retention time, surface area, perimeter, basin area, maximum depth, volume and water temperature. Reservoir age ranged from 7 to 75 years, surface area from 0.1 to 419.5 km^2 and retention time from 0.20 to 438 days. Detailed description along with features of each reservoir is presented in Table 1.

2.2. The Ecopath model

Ecopath with Ecosim (EwE—version 5.1.152) is based on the method of Polovina (1984), which estimates biomass and consumption of the different components of an aquatic ecosystem and uses network theory to analyze flows among components (Ulanowicz, 1986). A basic requirement of mass-balance models in Ecopath is that the input of each group must equal its output (equilibrium conditions). Then, a series of biomass budget equations are calculated for each group as follows:

Production − all predation on each group − non-predatory

mortality − all exports = 0

The resulting budget equations are transformed into simultaneous equations with the formula:

$$B_i \left(\frac{P}{B_i} \right) = \sum_{j=1}^{n} B_j \left(\frac{Q}{B_j} \right) - DC_{ji} + (B_i) \left(\frac{P}{B_i} \right) (1 - EE_i) + EX_i \qquad (1)$$

where B_i is the biomass of i; P/B_i is the production/biomass ratio of i that equals the total mortality rate (Z_i), as defined in fisheries (Allen, 1971); B_j is the biomass of predators; Q/B_j is food consumption per unit of consumer's biomass (j); DC_{ji} is the fraction of i in the diet of j; EE_i—ecotrophic efficiency, i.e., fraction of production of i that is consumed by predators or exported and usually ranges from 0.7 to 0.99; and EX_i is the export (i.e., catch) for any group (i). Therefore, a system with n groups will have n linear equations. As Ecopath links different groups through consumption, it allows the estimation of an unknown parameter for a given group.

2.3. Data source

In the 30 studied reservoirs (Table 1), two samplings on all biological groups were carried out; one in July and another in November 2001 (see Rodrigues et al., 2005a). Considering the purpose of the paper, models of the 30 reservoirs were standardized, every one with 15 compartments, to diminish the system complexity and to facilitate its comprehension and comparison (Hakanson, 1995; Martinez, 1991). This standardization avoids differences among models output values which could appear because species clustering method (Abarca-Arenas

Table 1
Characteristics of the 30 studied reservoirs in the State of Paraná, Brazil. Max. Dep. = maximum depth, T. R. = water retention time.

Reservoir name	River	Basin	Year	Basin Area	Area (km²)	Perimeter (km)	Max. Dep. (m)	T. R. (days)	Volume (km³)	Annual average temperature of water (°C)
Taquaruçu	Paranapanema	Paranapanema	1992	88000	80.10	156.35[a]	26.50	7.90	672.50	23.60
Capivara	Paranapanema	Paranapanema	1975	85000	419.30	738.93[a]	52.50	126.80	10540.00	23.70
Canoas II	Paranapanema	Paranapanema	1999	39556	22.50	65.81[a]	16.50	4.40	140.00	23.55
Canoas I	Paranapanema	Paranapanema	1999	40920	30.85	74.64[a]	26.00	6.00	207.00	23.95
Salto Grande	Paranapanema	Paranapanema	1958	38600	12.00	24.91[a]	9.20	1.40	44.20	21.95
Chavantes	Paranapanema	Paranapanema	1970	27500	400.00	401.84[a]	78.00	352.70	8795.00	21.90
Rosana	Paranapanema	Paranapanema	1986	99000	220.00	230.32[a]	26.00	18.60	1920.00	24.15
Alagados	Pitangui	Tibagi	1945	377	7.20	47.20	9.25	46.00	0.03	19.85
Apucaraninha	Apucaraninha	Tibagi	1958	513	2.00	16.90	–	12.00	0.02	–
Harmonia	Harmonia	Tibagi	1950	–	3.00	7.49[a]	12.00	–	8.00	20.90
Patos	Patos	Ivaí	1949	1086	1.30	3.20	5.75	0.20	<0.01	18.50
Mourão	Mourão	Ivaí	1964	573	11.30	60.00	12.70	70.00	0.06	20.95
Cavernoso	Cavernoso	Iguaçu	1965	1460	2.90	3.73[a]	8.30	–	–	19.50
Salto Santiago	Iguaçu	Iguaçu	1979	43900	208.00	376.99[a]	78.00	51	6753.00	21.60
Salto Osório	Iguaçu	Iguaçu	1975	45800	51.00	180.16[a]	43.00	16	1270.00	21.20
Salto Caxias	Iguaçu	Iguaçu	1998	57000	124.00	267.14[a]	53.00	31	3573.00	21.80
Foz do Chopim	Chopim	Iguaçu	1970	3800	2.90	5.25[a]	6.00	–	–	20.05
Jordão	Jordão	Iguaçu	1996	4700	3.40	21.74[a]	60.00	–	110.00	18.45
Curucaca	Jordão	Iguaçu	1982	–	2.00	3.70[a]	10.50	–	–	17.55
Foz do Areia	Iguaçu	Iguaçu	1980	29900	139.00	288.67[a]	135.00	102	5779.00	20.70
Passauna	Passaúna	Iguaçu	1978	–	14.00	35.30[a]	–	420.00	–	16.50
Piraquara	Piraquara	Iguaçu	1979	–	3.30	40.00	18.00	438.00	0.50	19.90
Salto do Vau	Palmital	Iguaçu	1959	340	2.00	–	3.50	–	<0.01	16.20
Iraí	Iraí	Iguaçu	2000	–	15.00	20.12[a]	8.50	240.00	–	20.00
Santa Maria	Piquiri	Piquiri	1950	–	0.10	–	4.30	–	–	16.70
Melissa	Melissa	Piquiri	1962	368	2.90	–	5.30	–	–	17.90
Guaricana	Arraial	Leste	1957	–	7.00	7.20	17.00	13.00	<0.01	19.95
Vossoroca	São João	Leste	1949	160	5.10	18.49[a]	12.50	–	0.04	19.00
Salto do meio	Cubatão	Leste	1931	252	0.10	3.90[a]	6.20	–	<0.01	18.35
Capivari	Capivari	Leste	1970	–	12.00	123.50	43.00	48.00	156.00	19.95

Sources: Júlio Jr. et al. (2005), Angelini and Gomes (2008), Companhia Paranaense de Energia Elétrica (2011), Comitê Brasileiro de Barragens (2011).

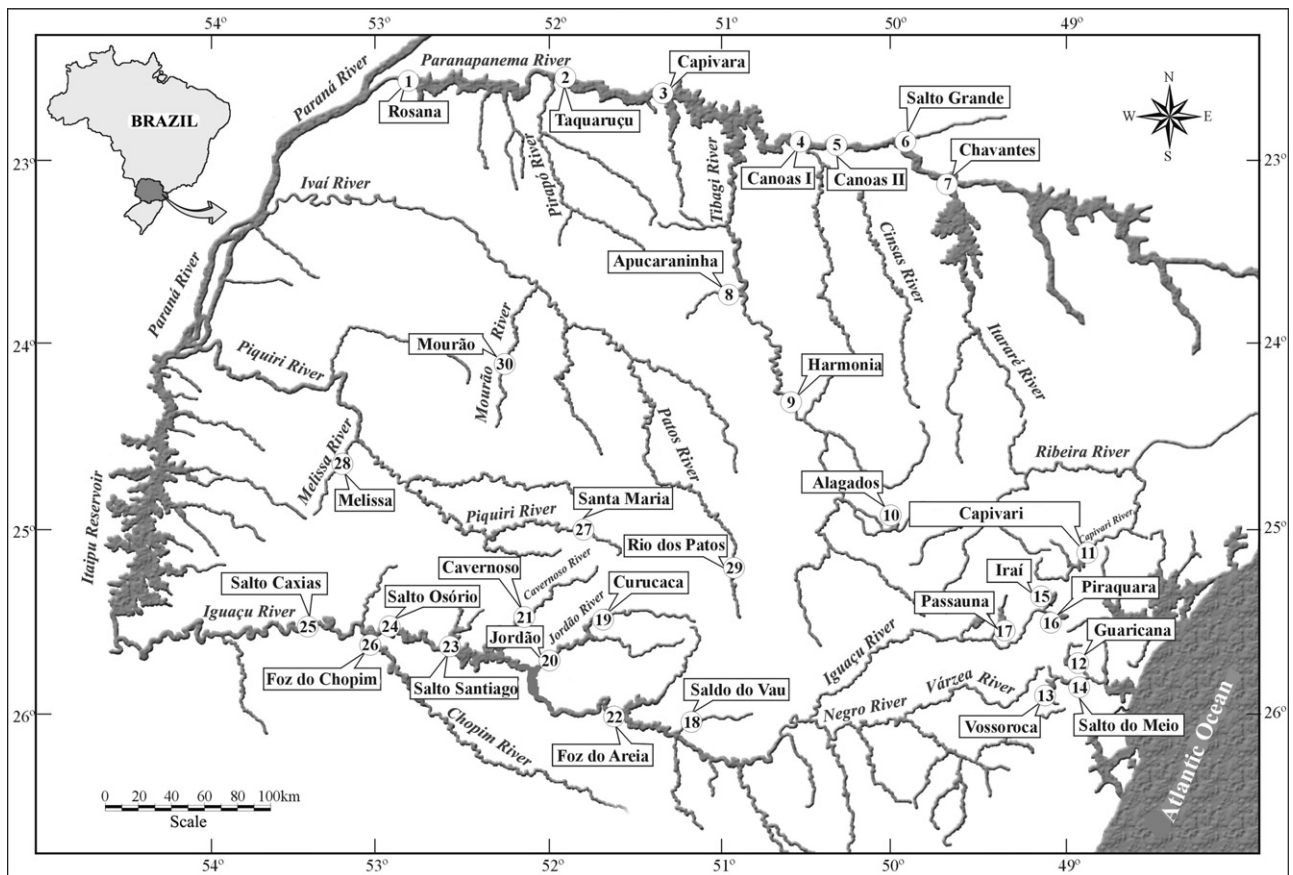[a] Perimeter (calculated using the software Google Earth™).

Fig. 1. Location of the 30 reservoirs studied in the State of Paraná, Brazil, sampled in July and November 2001.

and Ulanowicz, 2002). The data set was separated in two great broad groups: (i) 'non-fish' compartments: 1—phytoplankton, 2—periphyton, 3—rotifer, 4—cladoceran, 5—copepod, 6—bacteria, 7—protozoan, 8—benthos, 9—detritus; and (ii) 'fish' compartments: 10—omnivorous, 11—insectivorous, 12—piscivorous, 13—herbivorous, 14—detritivorous and 15—invertivorous.

All data required for Ecopath with Ecosim (EwE) were standardized to units of t km^{-2} or t km^{-2} yr^{-1} and data in other units were converted to tons (Jørgensen, 1986; Optiz, 1991). The standardization of biomass input data followed the procedures described below.

2.3.1. 'Non-fish' compartments

2.3.1.1. Phytoplankton and periphyton. Densities of the phytoplankton compartment (in mm^3 l^{-1}) are presented by Rodrigues et al. (2005c) and Train et al. (2005). Since most of this compartment occurs in the euphotic zone (km), the value of this depth multiplied by the reservoir area (km^2) gives the volume of water in the euphotic zone in km^3, which can be turned into m^3 (multiplied by 10^9). Thus, we can calculate the total phytoplankton multiplying the value of phytoplankton in mm^3 m^{-3} (mm^3 l^{-1} multiplied by 1000), by the euphotic volume (m^3). This result divided by the reservoir area (m^2) is the final value of phytoplankton in g m^{-2}, which is the same as t km^{-2}. We considered that 1 mm^3 equals 1 g (Optiz, 1991).

Periphyton data (data from algae adhered to submerged substratum) (Rodrigues et al., 2005b; Felisberto and Rodrigues, 2005) were sampled in mg cm^{-2} (or t km^{-2}); values observed for each reservoir were the input (without modifications) for the respective models.

2.3.1.2. Zooplankton. The zooplankton was divided into three groups (Lansac-Tôha et al., 2005): rotifers, cladocerans and copepods. We used the number of individuals m^{-3} transformed into g m^{-3} with a simple multiplication using the following criterion: one rotifer weighs on average 0.0005 g, whereas one copepod or cladoceran weighs 0.001 g (Optiz, 1991). Similarly as calculated for the phytoplankton, biomass estimate depended on the euphotic zone and the area of the reservoir.

2.3.1.3. Bacteria and protozoan. The basic unit used in bacteria and protozoan studies is the number of cells ml^{-1} converted into micrograms of carbon per liter (μg C l^{-1}) using data on biovolume. For calculations, we considered the average depth of the water column (km) multiplied by the reservoir area (km^2), which results in the total volume of the reservoir (km^3) and the conversion: 1 g of carbon is equivalent to 10 g of wet weight (g WW) for organic tissue (Optiz, 1991). Therefore, values in g ml^{-1} (transformed in g l^{-1}) were multiplied by the total volume and divided by the area, and resulted in g km^{-2} and then t km^{-2}.

2.3.1.4. Benthos. Data on benthos were directly computed in Ecopath, because the sampling method used (modified Peterson; Takeda et al., 2005a) estimated the density (number of individuals m^{-2}). In despite of the high variability of species, sizes and body shapes within this group, we assumed that each individual weighed 0.001 g wet weight (Optiz, 1991). Data were detailed in Takeda et al. (2005a,b) and Higuti et al. (2005).

Estimates for the parameters P/B (production/biomass), Q/B (consumption/biomass) and EE (ecotrophic efficiency) for all 'non-fish' compartments were based on the literature or empirical

Table 2
Database and standardized values of production/biomass (P/B) and consumption/biomass ratios (Q/B) for 'non-fish' compartments used to calculate in Ecopath the trophic structure of 30 reservoirs located in the State of Paraná, Brazil.

Compartments	P/B	Q/B	Database
Phytoplankton	183	–	P/B in Train and Rodrigues (1997), Thomaz (1991), Thomaz et al. (1997) and Gascuel et al. (2008); EE in Silva Jr. (1998)
Periphyton	2400	–	P/B in Rodrigues (1998) and Gascuel et al. (2008)
Zooplankton			
Rotifer	24	60	P/B in Angelini et al. (1996) and Gascuel et al. (2008); diet composition in Lansac-Tôha et al. (1997); Q/B in Sipaúba-Tavares et al. (1994)
Cladocera	12	30	
Copepoda	6	15	
Bacteria	360	600	P/B and Q/B in Šimek and Straškrabová (1992), Wetzel (1995) and Hall Jr. and Meyer (1998)
Protozoa	365	780	B, P/B in Optiz (1993)
Benthos	10.4	26	P/B in Brey (1999) and Morin and Bourassa (1992); diet composition and Q/B in Mihuc (1997) and Cummins and Klug (1979)

equations. Table 2 supplies estimates of PB and QB for every 'non-fish' component. Input values for these attributes were the same for all reservoirs, due to the lack of data on growth, production and consumption of the groups, which is observed for most of them in the tropics, in addition to some uncertainties in the taxonomic status of several species in the groups. Thus, differences for these groups are attributed by their respective biomass values sampled in the reservoirs. We opted to have the same number of compartments (structure) in all models, because all non-fish groups occurred in all reservoirs.

2.3.2. 'Fish' compartments

Fish were sampled in reservoirs using 20-m long gillnets (2.4; 3; 4; 5; 6; 7; 8; 9; 10; 12; 14 and 16 cm mesh sizes between opposite knots; effort was the same in all reservoirs. After identification of the species, they were grouped according to their trophic categories to standardize the number of compartments in the models. Stomach contents of the majority of species were analyzed for each reservoir (Gubiani et al., in press), and species were grouped into six trophic categories, based on values of percentage in volume (>50% of predominant items), as follows: omnivorous (when there was a predominance of plant and animal items in similar proportions), insectivorous (terrestrial and aquatic insects), piscivorous (fish), herbivorous (algae and/or higher plants), detritivorous (detritus) and invertivorous (benthic invertebrates). We also expect little effect of the standardization of the number of compartments for each reservoir, because each one of them represents a clear ecological function in the ecosystems. In addition, the ichthyofauna of the 30 selected reservoirs has similar origin (all belong to the Paraná River basin), with some differences only in the Iguaçu River (which has simpler ichthyofauna) (Abell et al., 2008). The diet composition matrices (DCi, Eq. (1)) were performed using a weighted mean of volume proportion of the items in the diet of species that composed the grouping. The number of species in each compartment varied among reservoir depending on local species richness (Fugi et al., 2005).

PB was calculated using the empirical regression of natural mortality (M) proposed by Pauly (1980), whereas QB was estimated following Palomares and Pauly (1998). We estimated values of P/B and Q/B for each fish species (see Gubiani et al., in press) and based on species abundances, we calculated the weighted mean of these parameters for each compartment (trophic category), following Angelini and Agostinho (2005a). Growth parameters of the species followed Angelini and Agostinho (2005b) and Gubiani et al. (2009). Biomass (B) was assessed in Ecopath (all EE's values were between 0.9 and 0.99) or, in some of cases, in virtual population analysis (VPA) using Fisat (Sparre et al., 1989; FAO-ICLARM, 1996), calculated for each species and then added to the category they belonged.

2.4. Quality of the data and model analyses

In general, calibration of EwE models was conducted using time series data of fishery data (Shannon et al., 2003). EwE was misused in the past, because models were calibrated without fitting values to a time series (Heymans et al., 2009). As studied reservoirs do not have fishing activity, it would be impossible to calibrate the models using this approach. However, at least for EwE steady-state models, it is possible to test the consistency of model outputs using the routine Ecoranger, which allows an evaluation of the quality of the input data through the Pedigree Index.

The Pedigree Index was estimated to quantify the appropriateness of each EwE model. In this routine, user can classify the quality and reliability of each input data attributing a value between 0 (information with low precision) and 1 (data and parameters consistent with local information) (Funtowicz and Ravetz, 1990; Christensen et al., 2005). EwE calculates the average of these values, which resulted in an overall Pedigree Index for the model, also varying from 0 (model with vagueness information) to 1 (model with accurate information). The Ecoranger routine considers input values as a mean from a normal distribution with a user-defined confidence interval. Thus, Ecoranger re-samples these input values, it runs over again models and tests the reliability of model outputs, which reduces inherent insecurity of input values and helps in the selection of the model that best fits to a given set of constraint (least squares, for example) (Pauly et al., 2000; Villanueva et al., 2006a). This is useful for finding better models for less accurate data (Christensen et al., 2005).

2.5. Ecosystems attributes for description of the models

EwE calculates several ecosystems attributes, but most of them are highly interrelated. In order to avoid this limitation, models were compared using a small set of ecosystem attributes distributed in five categories, according to Odum (1969): ecosystem bioenergetics, community structure, life history, recycling and overall homeostasis.

The first category is ecosystem bioenergetics, which was represented by Total Primary Production divided by Total Respiration (TPP/TR), Net Production of the Ecosystem (NPE = Total Production of the System minus Total Respiration) and CPUE (Catch Per Unit of Effort). TPP/TR is expected to be close to one in mature ecosystem and higher than one in system at early stages of development. A system grows by accumulating biomass, which can be expressed as Production minus Respiration. NPE should be lower in mature ecosystems because all production is used to maintain the system biomass. In addition, we used total CPUE (individuals per $1000 \, \text{m}^{-2}$ of gill nets in 24 h) as the estimator of yield (sensu Odum, 1969; net community production, yield), i.e., an index of secondary

Table 3
Values used (and/or estimated) in the basic parameterization in Ecopath, for 30 reservoirs in the State of Paraná, Brazil. Average (minimum–maximum values).

No.	Compartment	B (ton km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	Trophic level
1	Phytoplankton	335.41 (7.59–670.25)	183	–	0.29 (0.01–1)	1
2	Periphyton	99.62 (0.00–150.50)	2400	–	0.46 (0.00–1)	1
3	Rotifer	3.98 (0.37–5.09)	24	60	0.63 (0.02–1)	2.63 (2.20–2.90)
4	Cladocera	3.77 (0.03–7.14)	12	30	0.26 (0.00–1)	2.40 (2.12–2.61)
5	Copepoda	1.82 (0.05–3.22)	6	15	0.38 (0.08–1)	2.51 (2.14–3.13)
6	Bacteria	2.80 (0.29–4.28)	360	600	0.47 (0.00–1)	2
7	Protozoa	2.44 (0.05–5.08)	365	780	0.59 (0.00–1)	2.55 (2.00–3.00)
8	Benthos	4.00 (0.23–24.20)	10.4	26	0.80 (0.02–1)	2.55 (2.20–3.44)
9	Omnivorous	2.56 (0.02–11.10)	6.23 (0.39–25.30)	39.47 (6.24–111.80)	0.65 (0.06–1)	2.73 (2.11–3.59)
10	Insectivorous	2.33 (0.02–12.60)	4.55 (1.00–13.30)	23.23 (5.00–90.17)	0.67 (0.08–1)	3.40 (2.00–4.32)
11	Piscivorous	1.57 (0.35–6.01)	2.99 (0.21–10.30)	23.76 (4.60–71.75)	0.95 (0.31–1)	4.01 (3.17–4.90)
12	Herbivorous	2.96 (0.10–19.13)	8.16 (1.00–56.76)	29.26 (10.00–79.29)	0.57 (0.03–1)	2.02 (2.00–2.46)
13	Detritivorous	2.31 (0.02–9.86)	5.29 (0.48–14.65)	44.72 (6.97–148.80)	0.58 (0.09–1)	2.07 (1.00–2.48)
14	Invertivorous	2.26 (0.01–14.58)	2.16 (0.36–12.00)	20.02 (3.04–64.17)	0.66 (0.05–1)	3.43 (2.89–4.04)
15	Detritus	–	–	–	0.42 (0.02–1)	–

production, and consequently potential fishery production. CPUE is expected to decrease in old reservoirs, for the same reason as NPE does.

Another category (*sensu* Odum, 1969) is community structure, which could be evaluated through species richness (S), which is not a result from Ecopath, but could influence ecosystem dynamics and productivity (Tilman et al., 2001). To minimize the effect of reservoir area on species richness, we used residuals of a linear regression (Sres) between these variables, with area as the predictor and richness as the dependent variable.

Life history attributes can be expressed as niche specialization, life cycle size or individual size (Odum, 1969). In the present analysis, we used individual size, calculated as Total Biomass divided by Total Production (TB/TP). Low values are typical of immature stages, whereas high values are typical of mature stages of ecosystems (Christensen and Pauly, 1998).

Recycling in a system is one of the main categories highlighted by Odum (1969) and it was represented by Finn's cycling index (Finn%), which measures the proportion of total system throughput that is recycled (Finn, 1976). Theory states that mature systems have higher recycling rates and recover faster from perturbations (Vasconcellos et al., 1997).

The category overall homeostasis was characterized by the System Development Capacity (SDC), which is the total amount of information a system has for its own development multiplied by total system throughput, i.e., a measure of the potential development of an ecosystem (Ulanowicz, 1986); and an increase in SDC may indicate that the system became less mature (Shannon et al., 2009). An additional direct measure for quantifying homeostasis is Schrödinger's ratio (Schröd), obtained as Total Respiration divided by Total Biomass (Marchettini et al., 2008). It is a measure of entropy production and it is expected to be lower in mature systems, i.e., in a stabilized ecosystem more biomass is maintained per less unit of energy flow (Odum, 1971).

2.6. Association between ecosystem attributes and characteristics of the reservoirs

The eight ecosystem attributes (TPP/TR, NPE, Sres, CPUE, TB/TP, Finn, SDC, Schröd) were used as descriptors for each object (Ecopath model for each reservoir) and their estimates were summarized in a principal components analysis (PCA; Legendre and Legendre, 1998). All attributes, except for NPE and Sres, were log transformed before running the PCA. Only the axes with eigenvalues higher than one were analyzed (Criterion of Kaiser-Guttmann; Legendre and Legendre, 1998). Scores of the axes retained for interpretation were correlated (r Pearson coefficient, $p < 0.01$) with reservoir surface area, reservoir age, reservoir perimeter, basin area,

maximum depth, volume, water retention time, and water temperature (Table 1). To avoid any confounding effects of reservoir basin, we also evaluated this feature, looking for dot distribution patterns in the PCA.

3. Results

3.1. Calibration and basic estimates

After integrating basic input data, and assessing the impact of the variability of input values on output models using the Ecoranger routine (Christensen et al., 2005), we found that biomass of herbivorous, invertivorous and periphyton had to be modified. They presented the highest sensibilities (lower values of Pedigree Index) among the input data; especially periphyton, because it was not possible to estimate substrate area, and, consequently, the correct biomass of this group. For the other 'non-fish' compartments, fits were used for PB or QB. Diet composition was also modified to fit the models but only in few reservoirs, especially for groups that fed on periphyton.

Ecoranger results showed a range between 10 and 200 acceptable runs with Monte Carlo simulations for the 30 reservoirs, with the minimum sum of deviations varying from 6.98 to 58.69. This interval indicates robust adjustments to all models since there was no prominent dissimilarity between outputs needed to provide mass balance from the original inputs. The mean value of the Pedigree Index was 0.673 (values between 0.596 and 0.751), which indicates an acceptable quality of the models (Christensen et al., 2005; Villanueva et al., 2006a). Consequently input values are consistent and they produced coherent models.

3.2. Trends in selected ecosystem attributes

Basic parameters values, estimated by Ecopath and or input values, are presented as averages, minima and maxima for the 30 reservoirs (Table 3). The herbivorous compartment presented the highest average biomass, followed by omnivorous, insectivorous, detritivorous, invertivorous and piscivorous compartments. In general, P/B values were higher for lower trophic levels, in both 'non-fish' and 'fish' compartments. The highest P/B value was detected in Apucaraninha Reservoir for the herbivorous compartment (56.76 yr^{-1}) whereas the lowest was found in Harmonia Reservoir for the piscivorous compartment (0.21 yr^{-1}).

The consumption/biomass ratio (Q/B) showed a trend of higher values for the detritivorous compartment, followed by the omnivorous, herbivorous, piscivorous, insectivorous and invertivorous compartments, with the highest Q/B value for the detritivorous

compartment ($148.8\,\mathrm{yr}^{-1}$) in Rosana Reservoir and the lowest for piscivorous ($4.6\,\mathrm{yr}^{-1}$) in Harmonia Reservoir.

Values of 0.00 for *EE* were obtained for periphyton (Capivara, Taquaruçu, Salto Grande and Chavantes reservoirs), cladocerans (Capivara, Taquaruçu, Canoas I, Chavantes, Guaricana and Vossoroca reservoirs), bacteria (Capivara and Salto Grande reservoirs) and protozoan (Foz do Chopim Reservoir), which indicates that these compartments were not consumed, and not produced in these reservoirs, i.e., "ecotrophically" they were irrelevant in those reservoirs. PB and QB values for these components were the same for all reservoirs (Table 3); thus, differences for these groups (e.g. EEs values) are attributed to their respective biomass observed values. We believe that this limitation in our models could be an advantage because this procedure standardizes the values for "non-fish" compartments and the main outputs models could be credited to their biomass, to fish components and to respective diet composition which is detailed for species at each reservoir, and consequently for the trophic groups.

Ecotrophic Efficiency (*EE*) variations within fish compartments were high and dependent on reservoir (Table 3). For instance, omnivorous presented an *EE* of 1 in Capivara, Taquaruçu and Rosana reservoirs, whereas the lowest *EE* was recorded for Guaricana Reservoir (0.06). Although input data were standardized, each ecosystem has its own dynamics and diet composition matrix and thus, trophic levels of compartments diverge among reservoirs (Table 3). However, these values were similar to other Ecopath models, for the same trophic level, with overall estimates following Gascuel et al. (2008). For the 30 reservoirs modeled here, a high predation pressure was evident, since values of *EE* for the group piscivorous were equal to 1 for most reservoirs (except for Taquaruçu and Capivara).

3.3. Association between ecosystem attributes and characteristics of the reservoirs

There was a significant correlation between number of species (*S*) and reservoir surface area ($r = 0.45$; $P < 0.01$), which corroborates the classic theory of island biogeography (the larger the area, the higher the number of species). Residuals of linear model ($S = 14.2397 + 0.0283$ Area) showed no trend (assumption of homogeneity of variances met) and, therefore residuals can be used to evaluate community structure after removing the effect of area from the analysis.

Three PCA axes presented eigenvalues higher than 1 and represented 73% of data variability. Axis 1 of the PCA was positively

Table 4
Results of the principal components analysis (PCA) used to summarize the eight ecosystem attributes calculated for 30 reservoirs in State of Paraná, Brazil. Eigenvectors (correlation) for each variable and percentage of explanation (%) for each axis are also presented. The highest correlations with each axis are represented in bold face.

Odum's categories	Attributes	Axis 1	Axis 2	Axis 3
Community Energetics	NPE	**0.818**	0.358	−0.035
	TPP/TR	**0.600**	**−0.725**	−0.246
Community Structure	Sres	**0.703**	0.402	−0.318
	CPUE	0.484	0.137	−0.241
Life history	TB/TP	0.485	−0.160	**0.703**
Nutrient Cycling	Finn%	0.158	0.210	**0.728**
Overall homeostasis	SDC	**0.685**	0.488	0.011
	Schröd	**−0.717**	**0.693**	−0.073
	Eigenvalues	3.000	1.621	1.250
	%	37.500	20.268	15.631

correlated (Table 4) with four ecosystem attributes: NPE and TPP/TR (category: ecosystem bioenergetics), Sres (category: community structure) and SDC and Schröd (with this negatively) (category: homeostasis). Axis 2 was negatively correlated with TPP/TR and positively with Schröd ratio (Fig. 2a). Finally, axis 3 was correlated with the other two attributes: TB/TP (category life history) and Finn% which represent the cycling category (Fig. 2b). Thus, all PCA axes were correlated with Odum's five categories of attributes that identify ecosystem development.

Scores of the PCA axis 1 were negatively correlated with reservoir age (Table 5). There was no correlation between area and the axes retained for interpretation; hence, Sres removed the influence of area from richness. Although differences among basins were not clear in the ordinations (Fig. 2a and b), basin area and water temperature were positively correlated with axis 1. There were no significant correlations among axes and other features (Table 5).

4. Discussion

Most results from comparative studies on food webs have been misunderstood due to biases in fundamental units of comparisons resulted from scale problems, such as the definition of food web boundaries, the definition of 'trophospecies' (groups) and methods to evaluate feeding links (Winemiller, 2007). In this paper, all reservoirs and their components were sampled similarly. Besides, models were developed based on data obtained in the same research project; hence, the issues related to sampling
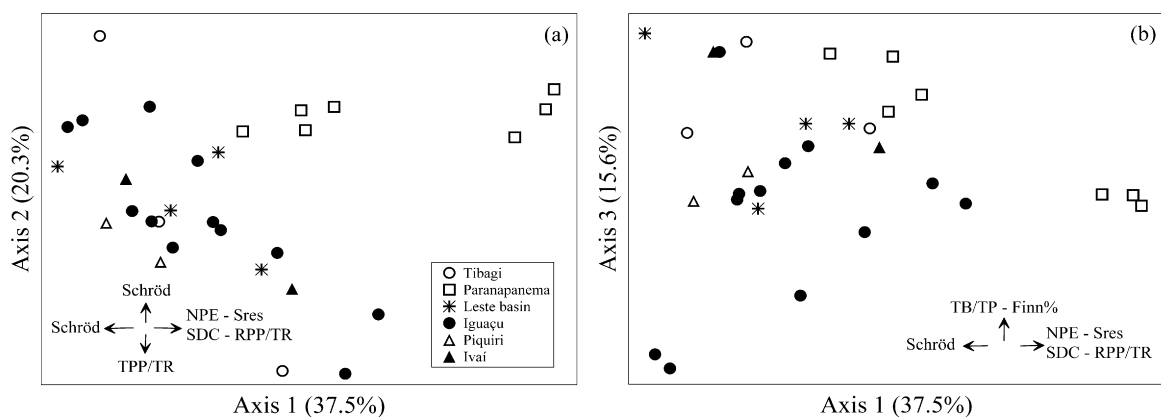

Fig. 2. Principal component analysis (PCA) applied to eight ecosystem attributes calculated for 30 reservoirs in the State of Paraná, Brazil. Reservoirs are classified according to river basins. Main attributes for each axis are highlighted and arrows indicate relation with axes: Schröd: Schrödinger's ratio; NPE: Net Production Ecosystem; Sres: Residuals from the linear regression between richness and area; SDC: System Development Capacity; TPP/TR: Total Primary Production/Total Respiration. The explanatory percentage (%) is also presented for each axis. (a) Axis 1 *vs.* Axis 2; and (b) Axis 1 *vs.* Axis 3.

Table 5
Correlation coefficients (and significant *P* values) among scores of the axes in the principal components analysis (PCA), and features of 30 reservoirs in the State of Paraná, Brazil.

Features	Axis 1		Axis 2		Axis 3	
	r	P	r	P	r	P
Surface area	0.25	0.181	0.26	0.167	0.29	0.126
Age	−0.62	0.000	0.04	0.813	0.36	0.050
Perimeter	0.26	0.197	0.15	0.449	0.24	0.228
Basin area	0.55	0.008	0.42	0.050	0.05	0.810
Maximum depth	0.23	0.240	−0.17	0.379	0.07	0.709
Volume	0.13	0.537	0.13	0.551	0.09	0.677
Water retention time	−0.23	0.399	−0.25	0.356	−0.09	0.739
Temperature	0.65	0.000	0.43	0.020	0.03	0.857

methods were minimized here. Furthermore, models have the same trophic compartments, what reduces possible aggregation problems and their outputs (Abarca-Arenas and Ulanowicz, 2002). This approach permitted us to compare and describe patterns of 30 reservoirs, and allowed us to study the development of these artificial environments.

A model is as good as the data used to parameterize and validate it (Heymans et al., 2009). Thus, the variability of the Ecopath models built in this study was determined with a sensitivity analysis (Pedigree Index and Ecoranger) available in the software (Christensen et al., 2005). Villanueva et al. (2006b) found for two African lagoons Pedigree indexes between 0.75 and 0.79, with sums of minimum deviations between 16.06 and 11.27. These Pedigree indexes values are a little higher than those found in this study (between 0.596 and 0.751). Villanueva et al. (2006a) also highlighted problems in the estimates made with input parameters taken from the literature and recommended to estimate them in specific studies. In the present study, Biomass, the most important input parameter in Ecopath, was estimated from sampled data, and PB and QB were calculated for all species (Gubiani et al., in press). Using these values and local species abundances, it was estimated a weighted mean of these parameters for the functional groups (compartments). These procedures minimized possible biases and resulted in consistent and reliable models.

The input parameter biomass of periphyton was modified for the 30 reservoirs, due to problems to estimate substrate area, diet composition and ecotrophic efficiency (*EE*). The periphyton usually shows higher doubt in Ecopath models (Rosado-Solórzano and Guzmán del Próo, 1998; Morales-Zárate et al., 2004; Angelini and Agostinho, 2005a; Villanueva et al., 2006a,b; Fetahi and Mengistou, 2007). Values of Ecotrophic Efficiency showed high predation pressure (piscivourous = 1), but groups from trophic level I (phytoplankton, periphyton and detritus) exhibited values close to zero, which indicate that they are underused. This may be a limiting factor to improve productivity in these ecosystems. However, low *EE* can also be related to the method used for the analysis of stomach contents, because we analyzed mainly adult fish (Fugi et al., 2005). Juveniles of herbivores that use better these resources were not analyzed. Fetahi and Mengistou (2007) found for the Awassa Lake (Ethiopia) that the phytoplankton is also little consumed by adult fish. However, Gomes and Miranda (2001a) showed a positive relation between phytoplankton and fish output, but theirs analysis were influenced by captures of tilapia, which is know to consume algae.

Considering the eight ecosystems attributes represented in the three PCA axes retained for interpretation, only CPUE (Catch Per Unit of Effort; the index of abundance or secondary production used to represent ecosystem bioenergetics) was not significantly correlated with these axes, showing that relative fish abundance does not seem to affect ecosystem development. In reservoirs, the temporal changes in fish abundance are influenced by alterations in primary productivity (Agostinho et al., 1999, 2008),

which is dependent of nutrients availability (Gomes and Miranda, 2001a,b).

Therefore, the nutrients reduction caused by transport and retention in the sediment affect directly the primary productivity and, consequently, the fish yields (Agostinho et al., 2007, 2008). Besides depletion in nutrients, the availability of its sources in the body of the reservoir is reduced by decomposition of the labile portions of the flooded vegetation (Agostinho et al., 2008), reducing the structural complexity of habitats and also decreasing reservoir carrying capacity (Gois et al., in press). This result may validate differences between growth and development in ecosystems: growth is the increase in biomass whereas development refers to how energy is used (Ulanowicz, 1986) and herein we are evaluating development, (CPUE is estimate for growth). In addition, contrary to another organisms, fishes are able to explore all environments at reservoirs, resulting in higher abundance variability because species explore on resources in different ways. Therefore, total CPUE value is a temporary condition and it is not a good indicator for ecosystem development.

Reservoir age was negatively correlated to axis 1, whereas TPP/TR and NPE were positively correlated. Consequently, both attributes decreased with time, as predicted by ecosystem development theory, i.e., the net production is lower in developed (aging) systems. As mentioned before, recent-formed reservoirs present increased primary productivity (Trophic upsurge period; Kimmel and Groeger, 1986; Okada et al., 1996), which is accompanied by an increase in net production or yield; however, as reservoirs age it is expected a decrease in production (Agostinho et al., 1999, 2008). According to Odum (1969) young ecosystems present high values of net community production, whereas mature ones presents low values.

Although Odum (1969) predicted that the number of species (richness) would increase with age, our results showed a positive correlation between Sres (regression residuals), which represent richness, and scores of axis 1, opposite to age. Hence, richness exhibited a negative correlation with age, a result expected for fish species in reservoirs (Agostinho et al., 1999). After the trophic upsurge period (Kimmel and Groeger, 1986; Kimmel et al., 1990; Agostinho et al., 2008) reductions in species richness are expected, due to the fact that some species are locally extinct, because they had not pre-adaptations for thriving in lentic environments (Fernando and Holčik, 1991; Gomes and Miranda, 2001b; Agostinho et al., 2008). In addition, older reservoirs should have lower richness when compared to young reservoirs (Agostinho et al., 1999). Some experiments have shown a strong positive correlation between the number of plant species and ecosystem productivity (Loreau et al., 2002; Tilman et al., 2001) and in general, it is assumed that diversity enhances ecosystem functioning (Loreau, 2000). So, in the present study, higher richness also means higher net production (NPE), which is lower in developed ecosystems or aged (old) environments. However, in reservoirs after the initial higher productivity (heterotrophic phase) occur progressive trophic depletion

and, consequently, decrease productivity. The gradual decomposition of flooded vegetation, as mentioned before, also contributes to the reduction in the availability of shelter and substrate for spawning or food organisms used by several species, mainly small fishes, contributing to reductions in species richness (Gois et al., in press).

The attributes that represented overall homeostasis (*sensu* Odum, 1969), System Development Capacity (SDC) and Schrödinger ratio (Schröd), showed opposite values when compared to Odum's ecosystem theory: SDC diminished and Schröd increased with age. Both attributes are associated with diminishing biomass over time. For example, fish productivity is high in recently formed reservoirs but decreases with reservoir aging, independently of catch effort (Agostinho et al., 2007). Thus, with lower biomass, Schrödinger's ratio (TR/TB) tends to increase and SDC, which has high correlation with total throughput of the system (Shannon et al., 2009), tends to decrease. Furthermore, contrary to age, water temperature was positively related to axis 1, and one of principle of ecology, appointed by Jørgensen and Fath (2004), is that order (structure) creating process diminish at diminishing temperatures, but the cost of maintaining the structure in form of disordering processes (respiration) could be not reduced in the same intensity that biomass (structure) is reduced. Also, reservoirs with higher temperatures tend to have increased microbial activity and decomposition, increasing the system respiration and consequently the Schrödinger ratio (TR/TB). However, these results need to be interpreted with caution, because temperature values of each reservoir were used in equations to calculate PB and QB values (Pauly, 1980; Palomares and Pauly, 1998) used as inputs in the models before running the simulations. The positive correlation between basin area and axis 1 seems to be spurious, given that the reservoirs located in larger basins do also have higher temperature.

Christensen and Pauly (1998) stated that complex theories, such as Odum's ecosystem development, stimulate research: "we like to think that setting up radical but testable hypotheses at the beginning had much to do with this progress". The quantification of Odum's theory, mainly using the software Ecopath, allows proper verification and validation of the theory. However, until now attributes related to ecosystem maturity were not correlated with age. This looks like a promising approach to advance ecosystem analysis, since we found a clear association between age and key principles of Odum's theory of ecosystem development.

What makes older reservoirs more mature, despite frequent and irregular human impacts aimed at generating hydroelectric power? We assume that all reservoirs are open systems, connected to and formed by a river, which constantly provides these systems with energy inputs. In addition, reservoirs work as nutrient sinks (decantation ponds) and become shallow environments, which are probably simpler and more stable (Agostinho et al., 1999). Nevertheless, the accumulated detritus may contribute to increase the abundance of detritivorous organisms. Those organisms may transform the grazing food web into a detritus food web, as previously stated by Odum (1969) for mature ecosystems. He also predicted that mature systems would have higher nutrient cycling. Moreover, higher nutrient cycling means increased resilience, as shown by Vasconcellos et al. (1997) for 15 coral reef environments. However, in our study, Finn cycling index was correlated with maturity just in the PCA axis 3, showing its lower importance for reservoirs ecosystem development.

Beyond Odum's perspective, Salthe (2002) defined the development of ecosystem as a predictable directional change, which occurs to reduce energy gradients and to produce entropy. These changes develop from immaturity (energy for growth) to senescence (energy for maintenance), concept a quite different from maturity since in senescence stage, regardless higher organization, ecosystem are more susceptible to perturbations because

mass-specific energy that could be used for recovery has declined and the system could suffer from information overload (Salthe, 2002). However, this could explain the apparent incongruent values of the attributes in the homeostasis category (Schröd and SDC) with ecosystem development theory found in our results, i.e., maturity in reservoirs could be a shorter period of early senescence, before susceptibility to perturbation becomes significant (Salthe, 2002).

The analysis presented here was based on eight attributes that describe entire systems. Hence, it is possible to conclude that maturity, or in better words, senescence, is an inherent characteristic of reservoir aging, regardless of human interference and reservoir area. Therefore, the results presented here are additional evidences of the importance of Odum's central theory of ecosystem development and also of the necessity to enhance it, with innovative perspectives (resembling DITT, developmental-infodynamic-thermodynamic theory from Salthe, 2002) and consistent evidences similar to those showed in this research. Therein, the reservoirs evaluated here do not seem to be mature, what suggests that in Neotropical reservoirs the nutrient input and temperature are responsible for delaying the aging process and/or to quickly senesce the ecosystems represented by the reservoirs.

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