

# Detrital food chain as a possible mechanism to support the trophic structure of the planktonic community in the photic zone of a tropical reservoir

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## ABSTRACT

### Detrital food chain as a possible mechanism to support the trophic structure of the planktonic community in the photic zone of a tropical reservoir

In the photic zone of aquatic ecosystems, where different communities coexist showing different strategies to access one or different resources, the biomass spectra can describe the food transfers and their efficiencies. The purpose of this work is to describe the biomass spectrum and the transfer efficiency, from the primary producers to the top predators of the trophic network, in the photic zone of the Riogrande II reservoir. Data used in the model of the biomass spectrum were taken from several studies carried out between 2010 and 2013 in the reservoir. The analysis of the slope of a biomass spectrum, of the transfer efficiencies, and the omnivory indexes, suggest that most primary production in the photic zone of the Riogrande II reservoir is not directly used by primary consumers, and it appears that detritic mass flows are an indirect way of channeling this production towards zooplankton. Accordingly, the optimal efficiencies in mass transfer between producers and consumers reflected by the slope of the biomass spectrum (close to -1), are not necessarily linked to the grazing chains, but may be the result of the coupling between several food routes (detritic and grazing) that start with primary production.

**Key words:** detritus, plankton, biomass spectrum, transference, body-size spectra

## RESUMEN

### La cadena alimenticia detritica un posible mecanismo de sostenimiento de la estructura de la comunidad planctónica en la zona fótica de un embalse tropical

En la zona fótica de los ecosistemas acuáticos, donde coexisten diferentes componentes de la comunidad con diferentes estrategias para acceder a uno o diferentes recursos, el espectro de biomasa puede describir las transferencias alimenticias y sus eficiencias. El propósito de este trabajo es describir el espectro de biomasa y la eficiencia de transferencia, desde los productores primarios hasta los principales depredadores de la red trófica, en la zona fótica del embalse de Riogrande II. Los datos utilizados en el modelo del espectro de biomasa se tomaron de varias investigaciones realizadas en este embalse entre 2010 y 2013. El análisis de los resultados de la pendiente del espectro de biomasa, de las eficiencias de transferencias, y de los índices omnivoría, sugieren que la mayoría de la producción primaria en la zona fótica del embalse Riogrande II es escasamente utilizada directamente por los consumidores primarios, y parece que los flujos de masa detriticos son una forma indirecta de canalizar esta producción hacia el zooplankton. De acuerdo con esto, las eficiencias óptimas en la transferencia de masa entre productores y consumidores reflejadas por la pendiente del espectro de biomasa (cercana a -1), no se deben necesariamente a la cadena de pastoreo, sino que pueden ser el resultado del acoplamiento entre varias rutas alimenticias

(*detritica y pastoreo*) que comienzan con la producción primaria.

**Palabras clave:** *detritus, plancton, espectro de biomasa, transferencia, espectro tamaño-cuerpo*

## INTRODUCTION

A food chain is the representation of the energy transfer among some organisms present in an ecosystem which, when interrelated with other chains, forms a complex system, the so-called “food web or trophic network”. It shows the interrelations between the structure of an ecological community, its stability and the processes occurring within an ecosystem. Ecosystem properties are not only determined by environmental changes, but are determined to a large extent by the functional roles and dietary strategies of the species present in the community (Tilman *et al.*, 1997, Kruk *et al.*, 2002). Studies on food chains focus mainly on the transfer of primary production to higher trophic levels. However, primary production that is not consumed by herbivores returns to the environment as detritus (necromass + heterotrophic microorganisms growing therein). This stock of detritus is an available source of resources that enters the detrital food chain and affects the trophic structure and dynamics of communities, and the maintenance of ecosystems (Hairston & Hairston, 1993). Thus, detritus in aquatic ecosystems may play an important role as a dynamic heterogeneous resource and habitat for many organisms.

The construction of reservoirs with the purpose of generating hydroelectric energy and drinking water in Colombia favored the performance of numerous limnological studies (Roldan, 2009). Most of these studies were carried out in the tropical reservoir Riogrande II, dealing with its physical and chemical water features (Montoya & Ramírez, 2007; Franco-Velázquez, 2011; Mazo *et al.*, 2015; Ramírez *et al.*, 2015), phytoplankton assemblages (Restano *et al.*, 2011; Bustamante Gil *et al.*, 2012; Hurtado-Alarcón & Polanía-Vorenberg, 2014; López-Muñoz, 2016; Palacio *et al.*, 2015; Ramírez-Restrepo, 2015) and zooplankton communities (Estrada, 2007; Villabona-González *et al.*, 2015).

Recent studies on the planktonic trophic chain

of Riogrande II reservoir suggested that the detritic pathway is the main route for energy flow in the reservoir (Ramírez *et al.*, 2015). The fraction of the phytoplankton biomass of smaller organisms that can be consumed by the dominant zooplankton is lower than 1 %, since 90 % of the estimated biomass of eukaryotic phytoplankton comes from a species of the genus *Staurastrum* (size  $\approx 70 \mu\text{m}$ ), whose size and morphology hinders grazing by the dominant cladoceran of genus *Bosmina*. In addition, biomass of the larger eukaryotic phytoplankton ( $> 20 \mu\text{m}$ ) flows mainly towards the detritic pathway being a source of dissolved carbon, and not to the consumers of higher trophic levels (López-Muñoz *et al.*, 2016).

Some models address a continuous distribution of biomass in an ecosystem as a function of a continuous of trophic levels (TL) and trophic transfer processes (Gascuel, 2005; Rochera *et al.*, 2017). To study the flow and transfers in the planktonic structure, the analysis of the biomass spectrum has been widely used to approach the planktonic food web structure (Sprules & Munawar, 1986). The existence of regular patterns in the planktonic biomass spectrum also allowed examining general energetic characteristics of food webs. This approach hypothesizes that the slope and shape of a biomass spectrum are determined by the rates of growth, respiration, and mortality, as well as by the trophic dynamics (Zhou & Huntley, 1997). The use of accumulated biomass together with body size is a possible approach to estimate the biomass spectrum. Size spectra analyses assume that biomass and production decrease progressively in heavier body-mass classes due to low transfer efficiency of carbon from prey to predators (Thiebaut & Dickie, 1992). This trophic continuum of size classes represents an empirically demonstrated pattern for plankton (Fry & Quiñones, 1994).

We hypothesize that, if the relationships between biomass and the trophic structure can be described, then the slope of the regression of the biomass spectrum at a given trophic level would

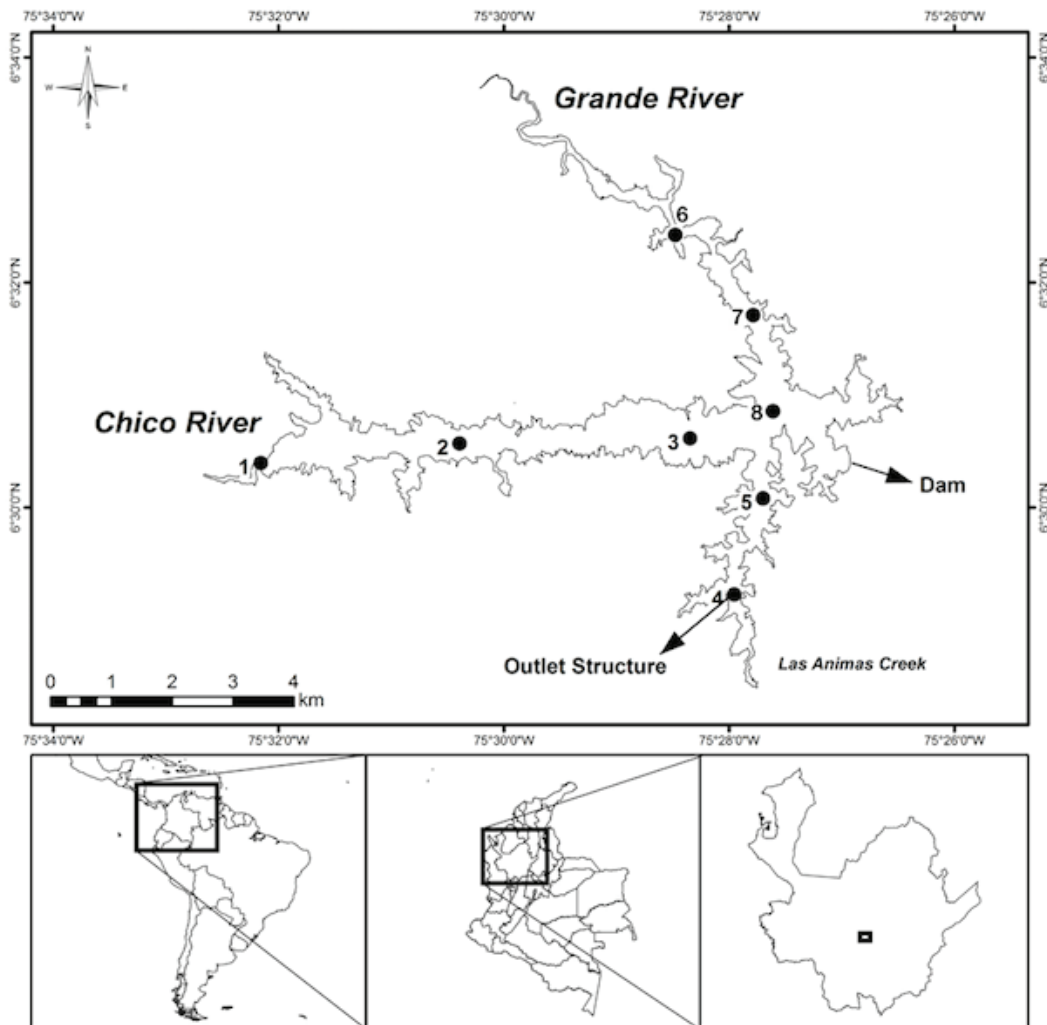
result from the relationship between the biomass production available and transfer efficiency of this biomass in the trophic network of the studied reservoir, being the detrital pathway flow the most important for sustaining the trophic structure (De Castro & Gaedke 2008).

Thus, in this study we aimed to further understand the planktonic trophic chain of Riogrande II tropical reservoir, and more specifically to investigate the relative importance of the grazing and detritic pathways by determining the biomass spectrum and the transfer efficiency from the primary producers to the top predators.

**METHODS**

**Study area**

The Riogrande II reservoir is located in Colombia, in the Rio Grande basin (latitude 6° 30' 50" N, longitude 75° 29' 10" W), at an altitude of 2270 meters above sea level. It can store a total volume of 240 million m<sup>3</sup>, and covers an average area of 12.14 km<sup>2</sup>. Its maximum and average depths (during the studied period) were 42.00 and 37.90 m, respectively, its maximum length was 10.00 km, and its retention time was 72.8 days on



**Figure 1.** Geographical location of Riogrande II reservoir and sampling stations (redrawn from Palacio-Betancurt, 2014). *Ubicación geográfica del embalse de Riogrande II y estaciones de muestreo (extraído de Palacio-Betancurt, 2014).*

average. Its multiple uses include hydroelectric power generation and drinking water supply (Restano *et al.*, 2011). Additional morphometric aspects can be found in Zabala (2013) and Palacio *et al.* (2015). The reservoir is mainly formed by water from the Grande and Chico rivers and Las Ánimas Creek (Fig. 1).

The data used in this study results from several studies carried out between 2010 and 2013 in the Riogrande II under the program "Study of the environmental problems of three reservoirs of *Empresas Publicas de Medellin* for the integral and adequate management of the water resources" (Palacio-Baena *et al.*, 2013; Toro *et al.*, 2013).

**Table 1.** Averages of the body sizes (individual) and biomass density reported for each of the planktonic functional types (PFT) within the planktonic trophic network, for the sampling campaigns evaluated in the Riogrande II reservoir. The biomass spectrum in relation to the body size of the organism generally predicts a relationship with the allometric form  $B_n \approx w_n^{-\alpha}$ ; with the body size being closely related to body weight ( $w_n$ ) (Platt, 1985). *Promedios de los tamaños corporales (Individuo) y la densidad de biomasa reportados para cada uno de los tipos funcionales planctónicos (PFT) de la red trófica planctónica para las campañas de muestreo evaluadas en el embalse Riogrande II. El espectro de biomasa en relación con el tamaño corporal del organismo generalmente predice una relación con la forma alométrica  $B_n \approx w_n^{-\alpha}$ ; estando el tamaño del cuerpo estrechamente relacionado con el peso corporal ( $w_n$ ) (Platt, 1985).*

PFTs	Body-size dw (mg x 10 <sup>-6</sup> ) per sampling campaign							
	sep-11	oct-11	nov-11	dic-11	jan-12	feb-12	mar-12	apr-12
Cyclopoids	1716.78	2007.60	1838.74	1755.07	1602.81	1909.77	1812.84	2269.15
<i>Asplanchna</i>	876.54	865.19	865.19	861.30	829.67	nd	880.29	843.73
Calanoids	9504.02	8822.38	9416.12	8656.00	8822.89	9454.44	9636.87	9691.04
Large cladocerans	2064.32	3028.11	2255.83	2148.53	2361.48	2971.00	2997.29	2490.83
Small cladocerans	1275.50	1349.33	1311.36	1347.33	1760.38	1843.16	1986.31	1584.89
Phyto<20um	0.09	0.08	0.10	0.07	0.09	0.09	0.12	0.10
Phyto>20um	5.13	1.98	2.25	6.13	2.04	3.71	2.01	2.94
	Biomass density dw (mg/m <sup>3</sup> ) per sampling campaign							
Cyclopoids	3.33	1.74	3.06	1.64	5.68	9.38	7.95	5.62
<i>Asplanchna</i>	4.28	11.13	13.07	12.44	5.80	nd	46.14	1.21
Calanoids	69.73	26.57	33.93	15.89	53.57	37.39	57.59	39.45
Large cladocerans	19.41	26.31	18.24	9.08	13.85	15.62	18.05	10.35
Small cladocerans	129.77	42.68	81.40	55.64	111.92	122.19	334.08	118.87
Phyto<20um	10.82	5.90	9.20	11.31	8.15	9.23	6.64	10.85
Phyto>20um	3964.08	131.10	242.92	1563.91	314.06	587.88	214.75	1431.48

Dry weight (dw). No data (nd)

Available information on Riogrande II reservoir includes that of: physical variables such as temperature and turbidity (Gómez *et al.*, 2013), nutrient dynamics nitrogen and phosphorus (Toro *et al.*, 2013), cyanobacterial assemblages (Palacio-Betancurt, 2014), eukaryotic phytoplankton (López-Muñoz, 2016) and metazooplankton (Villabona-González, 2015). Under this program, up to 24 field sampling campaigns were carried out from March 2010 to November 2013 at eight stations of the reservoir (Fig. 1). To perform the modeling of biomass spectrum and calculate transfer efficiency, the average of the biomass (phytoplankton and zooplankton) found in stations 1, 3, 4, 5 and 7 was here considered, according to the results summarized by Villabona-González *et al.* (2015).

**Body-size spectrum model**

Taxonomic categories as well as non-living organic matter (detritus) were assigned to Plank-

tonic Functional Types (PFTs). These PFTs include taxa of planktonic organisms that have similarities according to morphological characteristics, physiological and ecological affinity (Polovina, 1983; Christensen & Pauly, 1992). The information related to the consumption diets and growth rates of each PFT were taken from different sources (DeMott, 1982; Tolomeyev, 2002; Marten & Reid, 2007; Chang *et al.*, 2010; Giraldo, 2010).

Estimated biomass data (Table 1) standardized the biomass density by the width of the body size classes, according to Platt (1985). This method is particularly useful for the mathematical treatment and highlights the allometric basis for the biomass spectrum model. Body-size spectra are often presented as unnormalized biomass (B) in logarithmically scale size (w) intervals. The normalized spectrum  $B(w)$  can be estimated from these data by dividing each unnormalized biomass density  $M(w)$  by its corresponding body-size interval  $\Delta w$ . For simplicity, the

**Table 2.** Diet composition (relative frequency) of PFT consumers in the photic zone of Riogrande II reservoir. *Composición de la dieta (frecuencia relativa) de los PFT consumidores en la zona fótica del embalse Riogrande II.*

PFT Prey	Predator				
	Cycl	Aspl	Cala	L Clad	S Clad
Cyclopoid <sup>a</sup>	0.00	0.00	0.00	0.00	0.00
<i>Asplanchna</i> <sup>b</sup>	<b>0.04</b>	0.00	0.00	0.00	0.00
Calanoids <sup>c</sup>	<b>0.07</b>	0.00	0.00	0.00	0.00
Large cladocerans <sup>d</sup>	<b>0.07</b>	0.00	0.00	0.00	0.00
Small cladocerans <sup>d</sup>	<b>0.32</b>	<b>0.24</b>	0.00	0.00	0.00
Phyto>20µm	<b>0.50</b>	<b>0.75</b>	<b>0.93</b>	<b>0.93</b>	0.00
Phyto<20µm	0.00	<b>0.01</b>	<b>0.07</b>	<b>0.07</b>	<b>1.00</b>
<b>sum</b>	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>	<b>1.00</b>

a) Marten and Reid (2007); b) Giraldo (2010) and Chang *et al.* (2010); c) Tolomeyev (2002); d) DeMott (1982).

body-size ( $w$ ), the nominal value at which the normalized spectrum has to be estimated, is identified as the midpoint of each body-size interval on the logarithmic scale. The body-size intervals on the log scale are all set equal to  $\log 2$ . Thus:

$$\log B(w) \approx \log \left[ \frac{M(w)}{\Delta w} \right] = \log M(w) + \frac{1}{2} \log 2 - \log w$$

where,  $\Delta w = w\sqrt{2}$

The normalized biomass spectrum (Platt & Denman, 1977) or spectral density function, contains any range of specific body size. The continuous spectrum approach assumes that  $B_n dw_n$  is the increase in biomass corresponding to the increase in body size  $dw$ . We used logarithmic ordinal scales of biomass to illustrate patterns of variability of groups, as suggested by Sprules and Munawar (1986), and the programming language Python for general-purpose programming (see <https://www.python.org>).

Transfer efficiency (TE) is defined as the proportion of prey production ( $\text{mg m}^{-3} \text{ month}^{-1}$ ) that is converted to predator production ( $\text{mg m}^{-3} \text{ month}^{-1}$ ) ( $TE = P_j/P_i$ , where  $P_j$  is predator production and  $P_i$  is prey production) (Gascuel & Pauly, 2009).

If the transfer efficiency is optimal and is driven by a trophic chain of grazing and predation, then the values of the transfer efficiency (TE) and the slope of the spectrum will be close to 0.15 and -1, respectively. This agrees with Blazka *et al.* (1980) findings, who stated that, in freshwater food webs, TE is typically 0.15 from primary to secondary consumers (Blazka *et al.*, 1980). On the other hand, Brown *et al.* (2004) showed that the slope of the size spectrum should be close to -1 for optimized food webs, indicating simple energy considerations on an optimal efficiency of the transfer of resources from a trophic level to another.

Data obtained from several studies that have reported diet preferences of the planktonic taxa most commonly found in the Riogrande II reservoir (DeMott, 1982; Tolomeyev, 2002; Marten & Reid, 2007; Giraldo, 2010; Chang *et al.*, 2010) have been used to establish the coefficients of the trophic links among the main components of the

planktonic food web of the studied reservoir (Table 2).

### Biomass spectrum per trophic level

The biomass, generated by the photosynthetic activity of primary producers, enters the food web at trophic level (TL) = 1. Then, at TLs  $\geq 2$ , the biomass is composed by herbivorous, omnivorous, or predatory zooplankton, often with mixed diet and fractional TLs resulting in a continuous distribution of biomass along TLs (Lindeman, 1942). In our study, we defined the fractional "trophic level" *sensu* Odum and Heald (1975). The TL estimates for the reported taxa are calculated by assigning a TL of 1 to primary producers, and a trophic level of 1+ (the weighted average of the TL of the preys) for primary consumers, then similarly to other consumers at higher trophic levels. To perform the estimations, it is necessary to know the diet composition (DC), which is expressed as the proportion that each prey constitutes in the predator diet (Christensen & Pauly, 1992). This item is expressed as the relative proportion and the sum of the proportions of the different prey must be equal to 1, for each consumer (Table 2). DC, as referred, is based on literature information where the food preferences of each PFT are reported and scaled to the relative abundance of the prey in the photic zone of the Riogrande II reservoir (Table 2). The relative biomass of small Cladocerans, *Asplanchna* and Cyclopoids reported by Villabona-González *et al.*, (2015) were 61 %, 21 % and 1 %, respectively.

The biomass ( $B_j$ ) of a group of predators of body mass  $j$ , in a given time, is the result of its growth efficiency  $GE_j$  multiplied by its consumption  $Q_j$ . The latter, as a result of feeding of a biomass  $B_i$ , of a group of prey of body mass  $i$ , is given by

$$B_j = GE_j \sum Q_j \cdot DC_{ji}$$

where  $GE_j$  is the efficiency of assimilation of prey in predator body mass and  $Q_j \cdot DC_{ji}$  is the fraction of  $B_i$  that is captured by predator  $j$  (Christensen & Pauly, 1992).



With these assumptions, it is considered that the global biomass flow passes through the ecosystem from low to higher trophic levels through predation. Therefore, unconsumed prey would deviate towards the detritic pathways.

**Transfer Efficiency**

Transfer Efficiency (TE) describes the proportion of prey production that is converted into predator production (Christensen & Pauly, 1992). We used the following equation to calculate TE only among consumers,

$$TE_{ij} = \frac{P_j}{P_i}$$

where  $P_j$  is predator production and  $P_i$  is prey production.

Production estimations for the different PFTs (Table 3) were obtained from the monthly averages of the biomass densities (Table 1) and the growth rates reported in the literature (Gophen, 1978; Janicki & DeCosta, 1979; Robertson & Salt, 1981; Rodrigo *et al.*, 2007; Restano *et al.*, 2011).

**Omnivory**

The omnivory index (OI), a dimensionless variable, was calculated as the variance of the trophic

level of various predator-prey relationships (Christensen & Pauly, 1992), as follows:

$$OI_i = \sum_j (TL_j - (TL_i - 1))^2 \cdot DC_{ij}$$

Where

$TL_j$  is the trophic level of prey  $j$ ,

$TL_i$  is the trophic level of predator  $i$ ,

$DC_{ij}$  is the proportion of prey  $j$  in the predator's food  $i$ .

**RESULTS AND DISCUSSION**

The average biomass concentration and body weight of the PFTs (Planktonic Functional Types) in the photic zone of the Riogrande II reservoir shows a trend to reach maximum abundance at the lower end of the size spectrum, and exhibits a rapid decrease to a relatively tiny abundance in larger sizes (Fig. 2), as expected according to other studies (Sheldon *et al.*, 1972).

The slopes of the whole grazing size spectra (Slope With All =  $-1.04 \pm 0.2$ ;  $r^2 = 0.85$ ) were slightly steeper than the slope obtained when only including the autotrophic nanoplankton (Without Phyto > 20  $\mu\text{m}$ ); which was  $-0.89 \pm 0.08$  ( $r^2 = 0.90$ ), when data for the *Without Phyto > 20  $\mu\text{m}$*  food route was disaggregated (Fig. 2). Meanwhile, the slope of the predator biomass spectrum

**Table 3.** Averages of production estimated for the main predator-prey relationships between PFTs of the planktonic trophic network in the Riogrande II reservoir. Based on the monthly averages of the biomass densities (Table 1) and the growth rates reported in the literature (Gophen, 1978; Janicki & DeCosta, 1979; Restano *et al.*, 2011; Robertson & Salt, 1981; Rodrigo *et al.*, 2007), we estimated the production for these PFTs. *Promedios de producción estimados para las principales relaciones depredador-presa entre los PFTs de la red trófica planctónica en el embalse Riogrande II. Con base en los promedios mensuales de las densidades de biomasa (Tabla 1) y las tasas de crecimiento reportadas en la literatura (Gophen, 1978; Janicki & DeCosta, 1979; Restano et al., 2011; Robertson & Salt, 1981; Rodrigo et al., 2007) estimamos una producción para estos PFTs.*

PFTs	Production dw (mg m <sup>-3</sup> month <sup>-1</sup> )							
	sep-11	oct-11	nov-11	dic-11	jan-12	feb-12	mar-12	apr-12
Cyclopoids	6.07	3.18	5.59	2.99	10.37	17.11	14.51	10.26
<i>Asplanchna</i>	41.69	108.38	127.21	121.07	56.45	nd	449.11	11.79
Small cladocerans	1254.46	412.59	786.86	537.88	1081.93	1181.20	3229.44	1149.07

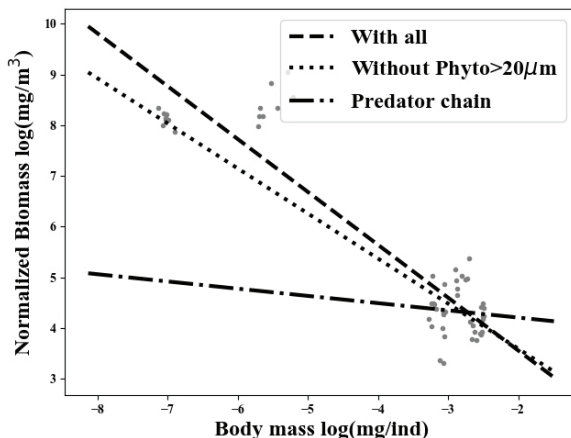
Dry weight (dw). No data (nd)

was  $-0.14$  ( $r^2 = 0.01$ ). As it was expected, and according to Brown *et al.* (2004), this reflects that the organisms devote some fraction of their metabolism to catabolism and activities associated to maintenance, and the remainder to anabolism and activities associated with production of new biomass, both by growth and reproduction.

Some studies argue that theoretically, the slope of a biomass spectrum is proportional to the ratio between the specific abundance change and individual body growth rates (Zhou & Huntley, 1997; Zhou, Carlotti, & Zhu, 2010). As such, less negative slopes are related to a high efficiency in the exploitation of primary production (Fig. 2), which does not occur in the grazing chains because the efficiency for this production to be channeled to other components of the trophic network depends not only on size (Burns, 1968), but also on its nutritional quality for predators (Galloway *et al.*, 2014).

The With All slope estimated ( $-1.04 \pm 0.2$ ) includes the body weight and the biomass of all the PFTs. Brown *et al.* (2004) predicted that the metabolic rate (MR) of organisms scales with body weight ( $w_n$ ) as  $MR \approx w_n^{0.75}$ . However, the true values of the allometric exponent and slope estimated are under debate. For example, in Lake Constance, phytoplankton and zooplankton exhibited an allometric exponent of 0.85 (De Castro & Gaedke, 2008), which would produce a slope of  $-1.1$  at a efficiency in mass transfer of 10 %.

The result of the estimated With All slope ( $-1.04 \pm 0.2$ ) is not sufficient by itself to support the hypothesis that the detritic pathway is the main route of the energy flow in the reservoir (Gaedke, 1993); because the optimal efficiencies in mass transfer between producers and consumers reflected by a slope of the biomass spectrum close to  $-1$  are not necessarily given by the grazing chains, but may also be the result of the coupling between several food routes (detritic and grazing) that start with primary production. In the Riogrande II reservoir, the biomass of nanophytoplankton (phytoplankton  $< 20 \mu\text{m}$  and  $> 3 \mu\text{m}$ ; Dussart, 1965) includes mainly Cryptophytes and other flagellated algae which are high quality food of adequate size for *Bosmina* (DeMott, 1982). However, the records of this biomass only reach around 1 % of the total



**Figure 2.** Biomass spectrum determined by the normalized biomass ( $\log \text{mg/m}^3$ ) as a function of the Body size ( $\log \text{mg/individual}$ ) for the photic zone of the Riogrande II reservoir based on the estimated biomass (dry weight) reported by Villabona-González (2015) and López-Muñoz (2016). The biomass spectrum in relation to the body size of the organism generally predicts a relationship with the allometric form  $B_n \approx w_n^{-\alpha}$ ; with the body size being closely related to body weight ( $w_n$ ) (Platt, 1985). *Espectro de biomasa determinado por la biomasa normalizada ( $\log \text{mg/m}^3$ ) en función del tamaño corporal ( $\log \text{mg/individuo}$ ) para la zona fótica del embalse Riogrande II, a partir de la biomasa estimada (peso seco) reportada por Villabona-González (2015) y López-Muñoz (2016). El espectro de biomasa en relación con el tamaño corporal del organismo generalmente predice una relación con la forma alométrica  $B_n \approx w_n^{-\alpha}$ ; siendo el tamaño del cuerpo estrechamente relacionado con el peso corporal ( $w_n$ ) (Platt, 1985).*

biomass in this reservoir (López-Muñoz *et al.*, 2016). This percentage seems a bit discouraging since this would be the potentially available food for *Bosmina*, the main zooplankter, whose high abundance could not be supported by this low amount of edible phytoplankton. The values found for the normalized biomass and the slope ( $-0.89 \pm 0.08$ ) of the spectrum, indicate that the biomass of these algae would be a limiting resource for organisms that consume these sizes, if this is its only food source. In the event that a high efficiency of predation occurred to sustain the *Bosmina* population, this fraction of phytoplankton would be almost extinguished from the photic zone of the Riogrande II reservoir, and likewise, the biomass of the small cladocerans would turn very low, which is quite far of reality. Most of the aquatic community size spectra



**Table 4.** Fractionated trophic levels and averages of accumulated biomass for each PFT in the photic zone of the Riogrande II reservoir, calculated from the estimated biomass reported by Villabona-González (2015) and López-Muñoz (2016). *Niveles tróficos fraccionados y promedio de biomasa acumulada para cada PFT en la zona fótica del embalse Riogrande II, calculado a partir de la biomasa estimada reportada por Villabona-González (2015) y López-Muñoz (2016).*

PFTs	TL	Biomass density dw (mg/m <sup>3</sup> )
Cyclopoids	2.51	4.80
<i>Asplanchna</i>	2.15	13.44
Calanoids	2.00	41.76
Large cladocerans	2.00	16.36
Small cladocerans	2.00	124.57
Phyto<20um	1.00	9.01
Phyto>20um	1.00	1056.27

Dry weight (dw)

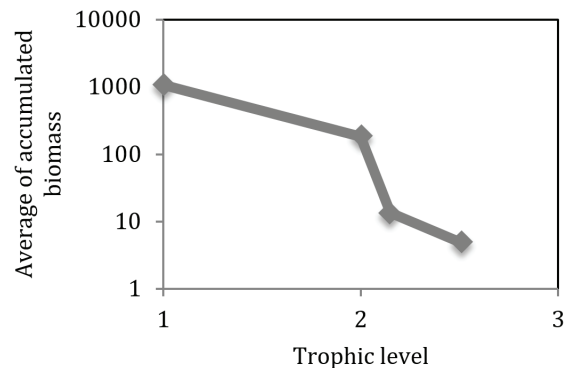
published so far for lakes only included phytoplankton, zooplankton, and occasionally fish (Sprules, 2008, Yurista *et al.*, 2014). In just few cases, protozoa and bacteria have also been included (Gaedke, 1993).

For the purpose of estimating the transfer efficiency only among consumers, we excluded phytoplankton from the calculation of the slopes. Compared to the other estimated slopes, the slope value decreased and gave rise to a less steep spectrum ( $-0.14 \pm 0.4$ ). This suggests the existence of alternative food routes other than grazing to support the food demand of zooplankton in the reservoir; the use of detrital food flows could then be an option.

Although detailed studies have not yet been carried out regarding the origin of the detritus in the studied reservoir, Ramírez *et al.* (2015) pointed out that in this system tripton (dead organisms, detritus and colloidal substances of organic or inorganic origin) and not phytoplankton is the component that mostly contributes to the attenuation of descending irradiance, which suggests a

high concentration of detrital particles. Accordingly, and taking into account the available prey biomass for Cyclopoids (see Table 2 and 4), we can infer that the value of this slope is not related to the low availability of food resources, but to the low consumption rates of the available prey. In this context, high concentrations of particulate organic matter could reduce the probability of encounter of a prey of high nutritional quality, even more if we consider that the majority of phytoplankton seems to be directed to the detritic pathway as being inedible (Table 4). These conditions support an eventual coupling between the grazing chain and that of detritus, supporting in a more stable way, the planktonic trophic network in the Riogrande II reservoir.

Platt (1985) argued that production within an ecosystem must be predictable from observations of the average density of biomass in any of the trophic positions. The biomass spectrum of total consumers per trophic level can be considered as the result of two processes: the first one is the biomass input towards TL = 2 (i.e. production of consumers through grazing), whereas the second would be the transfer of biomass from one TL to another at higher TLs (that is, predation). The density of biomass and the specific



**Figure 3.** Biomass spectrum determined by the average of accumulated biomass (dw, mg/m<sup>3</sup>) per trophic level for the photic zone of the Riogrande II reservoir, calculated from the estimated biomass (dry weight) reported by Villabona-González (2015) and López-Muñoz (2016). *Espectro de biomasa determinado por el promedio de biomasa acumulada (dw, mg/m<sup>3</sup>) en función del nivel trófico para la zona fótica del embalse Riogrande II, a partir de la biomasa estimada (peso seco) reportada por Villabona-González (2015) y López-Muñoz (2016).*

production of a community can be analytically related through a simple model of predator-prey dynamics, which shows how the biomass of predators results from the energy flow of prey biomass (Fig. 3). As shown in Figure 3 and Table 4, there is a change in the slope between TL 2 and 2.15. This supports our previous claims regarding low transfer efficiencies between primary consumers and the top predator (TL = 2.50) of the planktonic trophic network.

In addition, following the analysis by Dickie *et al.* (1987), a remarkable change in the slope of the distribution of biomass within TLs shows the inefficient transfer of energy from prey to predators. This inefficiency is easily described by the transfer efficiency (TE). Ware (2000) reviewed TE in marine and freshwater trophic networks, and estimated that TE is typically 0.15 from primary to secondary consumers in freshwater systems. The total carbon intake minus metabolic dissipation, is equal to the growth. Thus, the TE for all plankton is related to the community-assimilation efficiency at which biomass is transferred through several trophic levels. The results of the estimation of TE for the photic zone of the Riogrande I reservoir (Table 5) corroborate the hypothesis of low consumption of available prey and inefficiency in the transfer of energy from Small cladocerans to Cyclopoids. The TE results for the Cyclopoids-*Asplanchna* and *Asplanchna*-Small cladocerans relationships apparently reflect, however, an optimal TE (Table 5).

**Table 5.** Transfer efficiency calculated from the averages of production estimated for the main predator-prey relationships described. *Eficiencia de transferencia calculada a partir de los promedios de producción estimados para las principales relaciones depredador-presa descritas.*

Predator-prey relationships	Transfer efficiency	
	mean	sd
Cyclopoids-Small cladocerans	0.008	0.003
Cyclopoids- <i>Asplanchna</i>	0.190	0.307
<i>Asplanchna</i> -Small cladocerans	0.126	0.098

Standard deviation (sd).

The *Asplanchna*-Small cladocerans relationship is important when considering that this rotifer is omnivorous, whose feeding is dependent on the relative abundance of its preys, which also include phytoplankton. TE of this relationship does not reflect the direct consumption of small cladocerans, but the coupling between predation and grazing.

When the omnivory index value is zero, the consumer is fully specialized, that is, it feeds on a single trophic level; while non-zero values indicates that the preys for the consumer are found at different trophic levels. From the information used to calculate this index, two PFTs were identified that feed on more than two trophic levels, Cyclopoids and *Asplanchna*, with omnivory indices of 0.13 and 0.26, respectively. In particular, for omnivorous zooplankton, it is difficult to define their trophic position because they often show different preferences depending on a variety of factors such as, body size, the characteristic differences of prey organisms, and the availability of prey in their environments (Adrian & Frost, 2000).

Our results suggest that omnivory could be a generally stabilizing influence in communities, even though this is not yet associated with a formal model. However, in a reticulated trophic network, such as that found in the photic zone of the Riogrande II reservoir, omnivorous zooplankton can influence the composition of the community through a wide variety of trophic pathways.

From our study, it seems evident that the grazing food chain is less important than the detrital food chain. Likely, the inclusion of possible functional groups that interact in the detrital food chain, such as bacteria and protozoa, will make the omnivory index much higher than the value initially estimated, and there will probably be more PFTs with this feeding strategy. Although in this type of ecosystems there is a great fluctuation between trophic groups, it is likely that the replacements that may arise from the taxonomic groups within the planktonic community maintain the trophic tendency of the PFT described in this manuscript, with the detrital food chain subsidizing the scarce strength of the grazing chain for non-omnivorous organisms.

## CONCLUSIONS

The analysis of the slope of biomass spectrum suggests that most of planktonic production is scarcely used directly by primary consumers, and that detritic mass flows are an indirect way of channeling primary production to small cladocerans, like *Bosmina*, that largely dominated the community of primary consumers. Additionally, the low efficiencies in the transfer in the predator-prey relationship between Cyclopoids and small cladocerans show that the low biomass observed at the highest trophic levels are affected by a factor different from the density of their prey.

These considerations, together with the data on the small fraction of phytoplankton which could be available as a food source for *Bosmina*, as well as with the high observed biomass of this cladoceran, supports our conclusion that the detrital pathway main funnels the energy flow in the studied reservoir. Therefore, the coupling of the prominent flows of the detrital food chain with the low flows of the grazing food chain determine the structure of the planktonic community of the photic zone of the Riogrande II reservoir.

In Colombia, and in general in tropical areas, despite the amount of information that has been generated from studies aimed at describing the structure of planktonic communities, studies focused on ecological modeling of trophic interactions are still relatively scarce. Therefore, this study is a novel contribution and future studies are needed to continue exploring the causal relationships and the quantification of mass and energy flows in the aquatic ecosystems of this region.

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## Authors contribution

EAPG NRP, AP and AC designed the work, executed the process modeling and data analysis. EAPG and AC wrote the manuscript.

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