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ECOLOGÍA

SIMULATION OF BIOMASS DYNAMICS IN PLANKTON OF A HIGH-ALTITUDE ANDEAN TROPICAL RESERVOIR IN COLOMBIA

Simulación de la dinámica de la biomasa en plancton de un embalse colombiano tropical andino de alta montaña

Edison Andrés PARRA-GARCÍA[1]*, **Nicole RIVERA-PARRA**[2], **Boris A RODRÍGUEZ**[2], **Isabel Cristina HOYOS RINCÓN**[3]

[1] Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia, Calle 70 No. 52-21, Medellín, Colombia.
[2] Instituto de Física, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia, Calle 70 No. 52-21, Medellín, Colombia.
[3] Programa de Física, Facultad de Ciencias Básicas y Tecnologías, Universidad del Quindío, Carrera 15 con calle 12 norte, Armenia, Colombia.
* ***For correspondence:*** edisonparra50@gmail.com

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ABSTRACT

The understanding of the relationships between the planktonic communities in a reservoir allows us to infer possible changes in the redistribution of matter and energy flows in these systems. This work proposes a dynamic model for the trophic network of the Riogrande II tropical reservoir, which integrates the planktonic trophic chains of detritus and grazing, limiting the prey-predator interactions by introducing the prey meeting factor (*pmf*). We built a dynamic model of mass balance supported by an extensive bibliographic search. The limitations of consumers and resources were represented simultaneously by means of the *pmf*. The data used to validate the model were compiled from previous investigations carried out in this reservoir from 2010 to 2013. The values of *pmf* that we found in each simulation suggest that the top predator can access its main prey in certain concentrations of total phosphorus, with a probability of encounter ranging from 9.3 % to 17.7 %. Our simulations indicate that most of the primary production is poorly used by the primary consumers in the photic zone, however, it enters in the flows of the detrital chain and supports the production of zooplankton almost entirely. According to this finding, the biomass densities obtained in the previous studies can be better explained by the causal relationships assumed in this model.

Keywords: mass balance, mathematical model, prey-predator, reservoir, trophic webs.

RESUMEN

Entender las relaciones entre las comunidades planctónicas en un embalse nos permite inferir posibles cambios en la redistribución de los flujos de materia y energía en este sistema. Este trabajo propone un modelo dinámico para representar la red trófica del embalse tropical Riogrande II, donde se integran las cadenas tróficas de pastoreo y detritus y se limitan las interacciones entre predadores, presas y recursos al introducir un factor limitante de encuentro con la presa (*pmf*). El modelo dinámico se enfoca en el balance de masas sustentado en una amplia búsqueda bibliográfica. Los datos usados para validar el modelo se colectaron de datos previamente reportados para el embalse durante los años 2010 y 2013. Los valores de *pmf* obtenidos en cada simulación, sugieren que el predador dominante puede acceder a su presa principal a ciertas concentraciones de fósforo total, con una probabilidad de encuentro que va desde 9,3 % hasta 17,7 %. Nuestros resultados indican que la mayor parte de la producción primaria es poco aprovechada por los consumidores en la zona fótica, sin embargo, ingresa en el flujo de la cadena detrítica de manera que soporta la producción de zooplancton casi por completo. Las relaciones causales asumidas en este modelo explican en gran medida las densidades de biomasa reportadas en estudios previos.

Palabras Clave: balance de masas, embalses, modelo matemático, predador-presa, redes tróficas.

INTRODUCTION

Grazing and detritus food chains are the source of energy and nutrients for primary consumers in ecosystems. Detritus food chains are the main source of energy flow in many ecosystems because grazing herbivores use only a small portion of net primary production. Some studies have recognized the great importance of detritus food chains in ecosystems, but the theories of food webs and trophic dynamics have neglected this importance of detritus-based chains, and therefore, have focused almost exclusively on the grazing food chains (Moore *et al.*, 2004). Much of the detritus is consumed by bacteria, and this microbial production is linked with higher trophic levels through direct feeding from main consumers such as protozoa (e.g. heterotrophic nanoflagellates), that constitutes an intermediate link between bacteria and macrozooplankton (Sherr and Sherr, 2002). Consumers can affect the trophic structure so far, they diversify their diet, and the food quality of their prey is different. Some cladocerans such as *Bosmina*, for example, are selective consumers and in their diet, they prefer mainly *Cryptomonas* and secondly, small protozoa (DeMott, 1982), which belong to the chains of grazing and detritus, respectively.

According to the biomass reports from Riogrande II reservoir, made by Villabona-González *et al.* (2015), the small cladocerans reached a density of 1232 mg m^{-3} and the cyclopoid approximately 48 mg m^{-3}. Additionally, these authors observed that *Bosmina freyi* was a small dominant cladoceran of the zooplankton community. Almost simultaneously, López-Muñoz *et al.* (2016) concluded that the portion of the phytoplankton biomass that can be consumed by the dominant zooplankton in this system is less than 1 %. Parra-García *et al.* (2020) performed a biomass spectrum analyzes, showing that the most planktonic production of Riogrande II reservoir is low used directly for primary consumers and it seems that detritic mass flows are an indirect way of channeling primary production into primary consumers, like *Bosmina*.

The characteristic behavior of the principal source of feeding (here Small cladocerans) affects the consumer population (here Cyclopoids). These interactions (and others like the refuge effect of the prey) can be modeled by a set of first-order differential equations. The dynamic relationship prey-predator is one of the dominant topics in both ecology and mathematical ecology, due to its universal existence and importance (Berryman, 1992). Given that the probability of local extinction of a population in a system can be caused by difficulties in fitness, inbreeding, food access, and the evasion of predators or defense (Allee, 1931), the predator-prey models can be used to assess the hypothesis of whether the biomass of the top predator depends on the predation evasion ability of its prey (favored by the concentration of particulate material). If we take into account that the flow to the detritus pathway is the result of the death of all living organisms and unassimilated prey, and in ecosystems such as the photic zone of the Riogrande II reservoir the autochthonous production is the main source of detritus, then we hypothesized that i) the prominent flows of the detrital food chain mainly determine the coupling of the planktonic community in the photic zone of the Riogrande II reservoir, and ii) that the predator biomass top is the result of the subsidized flows of the detrital food chain and the probability of encounter of its prey, simultaneously.

Reservoirs receive and process the forcing forces of external variables from the drainage basin, generating a tendency towards compartmentalization and redistribution of matter and energy flows in the system (Margalef, 1983). In this way, these systems exhibit a hierarchical organization of organisms, whose structure and functionality respond to different spatial and temporal scales (Munkittrick and McCarty, 1995). In correspondence, the understanding of the relationships between the planktonic communities in a reservoir with spatial differences in the trophic state, provides insights about the possible alterations that could occur in the different compartments of the system, related to changes in the distribution of energy in the structure of the community (Odum and Barrett, 2006). In this paper, we propose a dynamic model for the Riogrande II reservoir that integrates the planktonic trophic chains of detritus and grazing to simulate the causal relationships between the main planktonic populations. We include data from previous studies to set-up and validate the model.

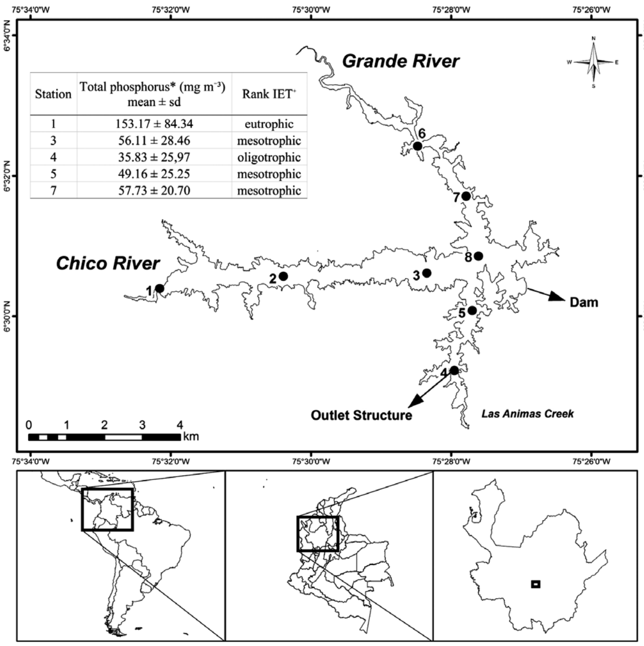
MATERIALS AND METHODS

Study area

Riogrande II reservoir is located in Colombia, in the Rio Grande basin (latitude 6° 30’ 50” N and longitude 75° 29’ 10” W), at an altitude of 2270 m. a. s. l. It was built between 1986-1988. This reservoir presents greater eutrophication near the rivers inlet and lowers in the areas close to the dam (Fig. 1). Riogrande II reservoir stores as much as 240 million m^3 and covers an average area of 12.14 km^2. Its maximum and average depths (during the sampling period) were 42.00 and 37.90 m, respectively. Its maximum length was 10.00 km, and its retention time was 72.80 days on average. The reservoir is mainly formed by the damming of water from the Grande and Chico rivers and Las Ánimas Creek (Fig. 1), and its uses include hydroelectric generation and drinking water supply (Restano *et al.*, 2011). The mean depth of the photic zone is 5 m. The corresponding volume, considered for the calculation of biomasses, is 70 million m^3. A detailed physicochemical report of the reservoir conditions can be found in Chapter 1 of Palacio-Betancourt (2014).

Diet composition

Taxonomic categories, as well as dead organic matter (detritus), were assigned to planktonic functional types (PFTs), which are the basic nodes in the food web. In addition



Station	Total phosphorus* (mg m^{-3}) mean ± sd	Rank IET^{+}
1	153.17 ± 84.34	eutrophic
3	56.11 ± 28.46	mesotrophic
4	35.83 ± 25,97	oligotrophic
5	49.16 ± 25.25	mesotrophic
7	57.73 ± 20.70	mesotrophic

Figure 1. Geographical location of the Riogrande II reservoir and sampling stations (modified from Palacio-Betancourt, 2014). The inset box shows the rank of Carlson's weighted trophic state index (IET) modified by Toledo *et al.* (1983). A total of 24 field sampling campaigns were carried out from March 2010 to November 2013 at eight stations. *From Palacio-Betancourt (2014). + From Villabona-González *et al.* (2015).

to detritus, these PFTs include taxa of planktonic organisms that have some similarities according to their morphological, physiological, and ecological characteristics, dietary habits, and/or similar life history (Polovina, 1983; Christensen and Pauly, 1992). Diet composition (DC) was based on information collected from literature (DeMott, 1982; Matz *et al.*, 2002; Marten and Reid, 2007; Chang *et al.*, 2010; Giraldo, 2010), and scaled to the relative abundance of the prey in the photic zone of the Riogrande II reservoir (Fig. 2).

The food preferences of each PFT have been reported for classified taxonomic groups by several authors (Fig. 2), we assume the following criteria to assign the feeding relationships between the PTFs modeled:

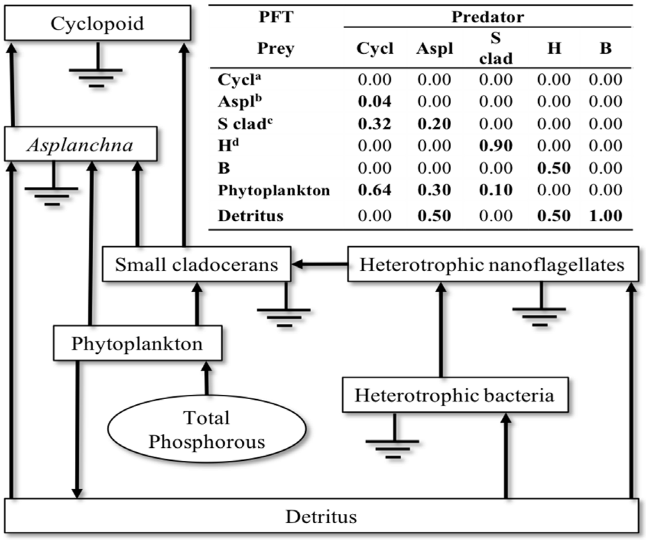
- **Cyclopoid.** Cyclopoid species tend to be plankton feeders, aggressive predators of consuming protozoa, rotifers, and small aquatic animals (Hutchinson, 1967). We assume for this model that the feeding of cyclopoids is constituted by the relative biomass proportion of their prey with respect to the rest of zooplankton. The relative biomass of Small cladocerans, *Asplanchna* and Cyclopoids is 61 %, 21 % and 1 %, respectively (Villabona-González *et al.,* 2015). In addition, cyclopoids that fed algae usually do not reproduce normally (Marten and Reid, 2007).
- **Asplanchna.** Some studies carried out at the Riogrande II reservoir have determined the rotifers of the genus *Asplanchna* as an omnivore, whose dietary preferences mainly depend on the relative abundance of the prey (Estrada, 1999; Giraldo, 2010).
- **Small cladocerans.** Feeding-selective small-sized is almost entirely represented by genus *Bosmina*. This was the dominant zooplankton taxon according to Villabona-González *et al.* (2015) and its dietary preference mainly depends on adequate size food for *Bosmina* (DeMott, 1982; López-Muñoz *et al.*, 2016).
- **Heterotrophic nanoflagellates (H).** Protozoa are recognized as major consumers of bacteria adhered to particles of organic matter in freshwaters (Bloem *et al.*, 1989; Berninger *et al.*, 1991).
- **Heterotrophic Bacteria (B).** Data of B and H biomass were estimated from the total bacterial content of carbon and numerical abundance of H in agreement with Hakspiel-Segura *et al.* (2015) for the Neusa reservoir.
- **Detritus.** Detritus are produced as a consequence of physiological processes and the death of algae. They are used by heterotrophic bacteria for their growth (Wetzel, 2001).
- **Phytoplankton.** For this model, the information on cyanobacteria biomass was included. The eukaryotic phytoplankton biomass was also included in this compartment.

Our conceptual model for the planktonic trophic web of the photic zone in the Riogrande II reservoir is presented in Figure 2. This model tries to describe most of the interactions in this area of the reservoir. The reactive soluble phosphorus available is a limiting nutrient for phytoplankton growth due to its low proportion with respect to total phosphorus (TP), and it is easily precipitable in neutral or slightly basic water. For this reason, we assume that TP is the determinant nutrient in the dynamics of growth for the PFTs densities in this system.

The model

We assume that dead phytoplankton cells are small and barely denser than water. Therefore, the debris moves towards the sediments with a slow sinking rate, in such a way that a large part of dead phytoplankton is colonized by bacteria before reaching the bottom (Jørgensen and Bendoricchio, 2001). In the Riogrande II reservoir, the estimated fraction of phytoplankton that is not filtered by the dominant zooplankton due to its small size is greater than 98 % (López-Muñoz *et al.*, 2016). Therefore, the dead phytoplankton enters to detritic trajectory, becoming the fundamental route of the energy flow in this reservoir (Parra-García *et al.*, 2020). The model describes the coupling of both food chains, as well as the causal relationships between the groups (Fig. 2).

Our model is based on the mass balance of seven groups, where the biomass flow of each group is calculated as the difference between incoming and outcoming flows. The



PFT	Predator				
Prey	**Cycl**	**Aspl**	**S clad**	**H**	**B**
Cycl[a]	0.00	0.00	0.00	0.00	0.00
Aspl[b]	**0.04**	0.00	0.00	0.00	0.00
S clad[c]	**0.32**	**0.20**	0.00	0.00	0.00
H[d]	0.00	0.00	**0.90**	0.00	0.00
B	0.00	0.00	0.00	**0.50**	0.00
Phytoplankton	**0.64**	**0.30**	**0.10**	0.00	0.00
Detritus	0.00	**0.50**	0.00	**0.50**	**1.00**

Figure 2. Conceptual model of the planktonic trophic network for the photic zone of the Riogrande II reservoir. The boxes represent the biomass of the modeled PFTs. The arrows indicate the direction of the flows. The inset frame shows the diet composition (relative frequency) of PFT consumers in the photic zone of Riogrande II reservoir. Cyclopoids (Cycl), *Asplanchna* (Aspl), Small cladocerans (S clad), Heterotrophic nanoflagellates (H), Heterotrophic bacteria (B). [a]Marten and Reid (2007). [b]Giraldo (2010) and Chang *et al*., (2010). [c]DeMott (1982). [d]Matz *et al*. (2002).

incoming flows are constituted by primary production, prey assimilation by predators, and detritus flow (in B and H). On the other hand, the outflows are accounted for predator's consumption, flow to detritus, and eliminations by sinking and respiration.

The governing equations below describe the changes in relative density of producers and consumers, respectively.

$$\frac{dP}{dt} = PP - \epsilon_S \gamma_{S,P} 0.01P - \epsilon_A \gamma_{A,P} P - \delta_P P; \tag{1}$$

$$\frac{dD}{dt} = \delta_P P - \epsilon_B \gamma_{B,D} D - \epsilon_H \gamma_{H,D} D - \epsilon_A \gamma_{A,D} \frac{D}{P} - \delta_D D; \tag{2}$$

$$\frac{dS}{dt} = \epsilon_S \gamma_{S,P} 0.01P + \epsilon_S \gamma_{S,H} H - \epsilon_A \gamma_{A,S} AS - \epsilon_C \gamma_{C,S} \varphi CS - \delta_S S; \tag{3}$$

$$\frac{dA}{dt} = \epsilon_A \gamma_{A,S} AS + \epsilon_A \gamma_{A,P} P + \epsilon_A \gamma_{A,D} \frac{D}{P} - \epsilon_C \gamma_{C,A} \varphi CA - \delta_A A; \tag{4}$$

$$\frac{dC}{dt} = \epsilon_C \gamma_{C,S} \varphi CS + \epsilon_C \gamma_{C,A} \varphi CA - \delta_C C; \tag{5}$$

$$\frac{dB}{dt} = \epsilon_B \gamma_{B,D} D - \epsilon_H \gamma_{H,B} B - \delta_B B; \tag{6}$$

$$\frac{dH}{dt} = \epsilon_H \gamma_{H,B} B + \epsilon_H \gamma_{H,D} D - \epsilon_S \gamma_{S,H} H - \delta_H H, \tag{7}$$

where, P is Phytoplankton, D is Detritus, S is Small cladocerans, A is Asplanchna, C is Cyclopoid, B is Heterotrophic Bacteria, and H is Heterotrophic nanoflagellates. The values of the parameters used in the equations are described in Table 1.

In this model, the limitations of consumers and resources simultaneously play an important role that is represented by a parameter that we call *prey meeting factor* (*pmf*). This parameter measures the probability of an encounter between the cyclopoid predator and its prey. The *pmf* parameter can produce a functional response depending on the detrital organic matter concentration, stabilizing or destabilizing the system. Therefore, taking into account the dynamical analysis made over the model, the *pmf* has been adjusted around the non-zero fixed point from 0.093 to 0.177.

The biomass input for each compartment was calculated according to the equations of Peters (1986) and adjusted to the relative biomass of the zooplankton PFTs.

The normal zooplankton biomass (NZB) in a given lake it is calculated as (Peters, 1986):

$$\text{NZB} = 38 * \text{TP}^{0.64} \tag{8}$$

However, this value must be scaled according to the relative biomass of Small cladocerans, *Asplanchna*, and Cyclopoids as 61 %, 21 %, and 1 %, respectively (Villabona-González *et al*., 2015). Equation (8) is modified as follows:

$$\text{NZB} = \text{relative\_biomass\_ zooplankton} * (38 * \text{TP}^{0.64}) \tag{9}$$

Here, we assume that nutrients released by microbial mineralization are not available to phytoplankton. Similarly, we assume that the amount of detritus caused by consumers through excretion or mortality without depredation is very low compared to the generated by phytoplankton, therefore, this amount is not taken into account in this model. In addition to the losses related to consumption, other losses (i.e., elimination) of biotic PTFs are included, which are primarily related to respiration. We specify a rate of loss of detritus from the system by sedimentation (sinking = 0.05 day^{-1}) (Jørgensen and Bendoricchio, 2001).

Numerical analysis

Our model describes the biomass flows through the trophic levels, defined mainly by the food strategy. The populations are regulated by the available resources and the spatial variation of the consumers relative biomass. The system equations are solved based on the annual variation of the phosphorus concentration for each station sampled (Fig. 1), and such results are compared with the values reported by Villabona-González *et al*. (2015).

The metabolic characteristics of the organisms and their biomasses can be determined in laboratory conditions by assuming the stable state of the system without consumers, without considering the common interactions in an

Table 1. Parameter values used in the equations. The values of the parameters and state variables that were not collected directly from the field observations were obtained from what is reported in the literature. The parameters without units are dimensionless.

Parameter symbol	Value (units)	Name	Reference
$\gamma_{S,P}$	$\frac{NB_s}{PP}$	Consumption rate of S in P	(DeMott, 1982; López-Muñoz *et al.*, 2016)
$\gamma_{A,S}$	$\frac{0.2}{NB_A}$ (m³ mg⁻¹)	Consumption rate of A in S	(Estrada, 2007; Chang *et al.*, 2010; Giraldo, 2010)
$\gamma_{A,P}$	$\frac{NB_A}{PP}$	Consumption rate of A in P	(Estrada, 2007; Chang *et al.*, 2010; Giraldo, 2010)
$\gamma_{C,A}$	$\frac{0.04}{NB_C}$ (m³ mg⁻¹)	Consumption rate of C in A	(Hutchinson, 1967; Marten and Reid, 2007)
$\gamma_{C,S}$	$\frac{0.32}{NB_C}$ (m³ mg⁻¹)	Consumption rate of C in S	(Hutchinson, 1967; Marten and Reid, 2007)
$\gamma_{B,D}$	0.5	Consumption rate of B in D	(Wetzel, 2001)
$\gamma_{H,B}$	0.5	Consumption rate of H in B	(Matz *et al.*, 2002)
$\gamma_{S,H}$	$\frac{NB_S}{NB_H}$	Consumption rate of S in H	(DeMott, 1982)
$\gamma_{A,D}$	$\frac{NB_A}{0.98}$ (mg m⁻³)	Consumption rate of A in D	(Estrada, 2007; Chang *et al.*, 2010; Giraldo, 2010)
$\gamma_{H,D}$	0.5	Consumption rate of H in D	(Matz *et al.*, 2002)
ϵ_A	0.19 (day⁻¹)	Assimilation rate of food in A	(Walline *et al.*, 1993)
ϵ_S	0.19 (day⁻¹)	Assimilation rate of food in S	(Walline *et al.*, 1993)
ϵ_C	0.1 (day⁻¹)	Assimilation rate of food in C	(Walline *et al.*, 1993)
ϵ_B	0.3 (day⁻¹)	Assimilation rate of food in B	(Del Giorgio and Cole, 1998)
ϵ_H	0.19 (day⁻¹)	Assimilation rate of food in H	(Weisse, 1991)
δ_P	0.98 (day⁻¹)	Elimination rate of P	(López-Muñoz *et al.*, 2016)
δ_C	0.8 (day⁻¹)	Elimination rate by respiration of C	(Del Giorgio and Cole, 1998)
δ_S	0.7 (day⁻¹)	Elimination rate by respiration of S	(Del Giorgio and Cole, 1998)
δ_H	0.7 (day⁻¹)	Elimination rate by respiration of H	(Del Giorgio and Cole, 1998)
δ_D	0.05 (day⁻¹)	Sinking rate of D	(Jørgensen and Bendoricchio, 2001)
δ_B	0.5 (day⁻¹)	Elimination rate by respiration of B	(Del Giorgio and Cole, 1998)
δ_A	0.7 (day⁻¹)	Elimination rate by respiration of A	(Del Giorgio and Cole, 1998)
φ	0.093 to 0.177	Prey meeting factor	Adjusted
TP	70	Annual average of total phosphorus	(Palacio-Betancourt, 2014)
PP	$30\times TP^{1.4}$ (mg m⁻³)	Primary production	(Peters, 1986)
NB_s	$0.61\times 38\times TP^{0.64}$ (mg m⁻³)	Normalized biomass of S	(Peters, 1986)
NB_A	$0.21\times 38\times TP^{0.64}$ (mg m⁻³)	Normalized biomass of A	(Peters, 1986)
NB_C	$0.01\times 38\times TP^{0.64}$ (mg m⁻³)	Normalized biomass of C	(Peters, 1986)
NB_H	$17\times TP^{0.71}$ (mg m⁻³)	Normalized biomass of H	(Peters, 1986)

ecosystem which affect production rates, metabolism, and consumption under natural conditions. The magnitude of the predation effect on the other components of the food web (i.e., the interaction force) was calculated from a cluster of *pmf* and different TP values (Fig. 1). The intensity of the effect is reflected in the equilibrium biomass of a given component in the presence of the predator.

The model initially accounts for the zooplankton and phytoplankton PFTs. Once the model reaches the stable equilibrium of the system, the additional components were introduced one by one. The order of incorporation was detritus, heterotrophic bacteria, and heterotrophic nanoflagellates. The system was allowed to settle into 30 days before the next component was introduced. The final system was simulated until a stable equilibrium was reached, or until no component reached zero biomass. This technique of assembling for the food web avoids the initial conditions problem, in which one or more components collapsed at very low densities with long recovery times. The *pmf* was adjusted by trial and error until the calculated biomasses of the stocks tended to stabilize from the first 30 days until the end of the simulation. Also, data of B and H biomasses were compared from other studies conducted in Colombian high-altitude Andean systems (Hakspiel-Segura *et al*., 2015).

RESULTS

We use the differential equations that describe the model and an average value of TP (70 mg m^{-3}) as the input of nutrients, which corresponds to the average concentration reported for the reservoir during the sampling period. Based on this concentration, we adjusted the value of the *pmf* at the threshold where the biomasses calculated were within the range of biomass observed (Fig. 3).

At a concentration of TP = 70 mg m^{-3} and a *pmf* = 0.132, the biomasses calculated from the modeled groups reach to values that are within the ranges of biomass observed for each one of them (Table 2 and Fig. 3). Based on the model results, we evaluate how the phytoplankton biomass that is not consumed and enters the detrital path, is sufficient for the detritivorous to transfer this biomass and sustain the food demand of higher trophic levels. The biomasses calculated from the phytoplankton in the modeled stations, are a result of simulating the effect of the limiting nutrient (in this case TP) in the primary production for the reservoir. According to the input variables of the model, it was expected that in the station with the highest concentration of total phosphorus (station 1 in Fig. 1), the calculated biomass densities of phytoplankton would be higher than in the rest of the stations.

We simulate the dynamics of the biomasses of each PFT for each station (with its respective average TP concentration) and obtain the equilibrium points of the simulation. Each point is stable when at the end of the simulation the stock is greater than zero, and unstable when the opposite occurs. For example, when in the simulation we only considered 1 % of the phytoplankton biomass, the calculated biomass of the cladocerans and the copepods reached to zero. On the contrary, if we eliminate all the connections of the grazing chain, the flows of the detritus chain are high enough to reach values close to the calculated biomass. Therefore, we adjust the pmf (value between 0.093 to 0.177) to obtain the expected results for the calculated biomass (Table 2). In summary, the equilibrium points of the simulation were adjusted based on the observed biomass of the PFTs that represent the highest trophic levels of the web, allowing a more integrative response to the mass transfer of the planktonic trophic web.

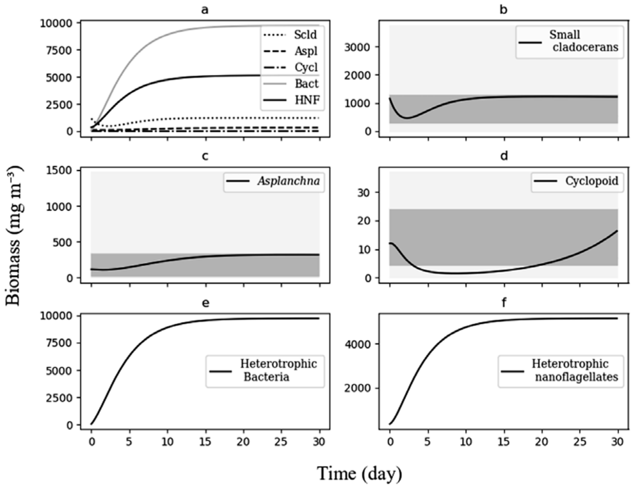


Figure 3. Biomasses simulated by model for 30 days of the planktonic trophic network in the Riogrande II reservoir. We used for this general model a concentration of TP = 70 mg m^{-3} and a *pmf* of 0.132. a) All consumers; b) Biomass calculated of Small cladoceran, in gray ranges of quartiles of biomes observed and reported by Villabona-González *et al*. (2015); c) Biomass calculated of *Asplanchna*, in gray ranges of quartiles of biomes observed and reported by Villabona-González *et al.* (2014); d) Biomass calculated of Cyclopoid, in gray ranges of quartiles of biomes observed and reported by Villabona-González *et al*. (2015); e) and f) Biomass calculated of heterotrophic bacteria and nanoflagellate, respectively.

DISCUSSION

In this model, primary and secondary productions are determined by the concentration (availability) of the limiting nutrient (TP) and the transfer efficiencies (quality of prey). In addition, the model is sensitive within the range of the mean values of the total phosphorus concentrations (36 to 153 mg m^{-3}) evaluated in the photic zone of the reservoir. Here, the percentage of net primary production that is not consumed by the grazing chain enters to the detritic chain (Fig. 2).

In our model, the equilibrium points of the simulations were stable only in the runs where the detrital chain was included alone or in combination with the grazing chain. If we eliminate all the connections of the chain of detritus,

Table 2. Comparison of observed (López-Muñoz, 2016; Palacio-Betancourt, 2014; Villabona-González *et al.*, 2015) and calculated biomasses (simulation model of biomass for 30 days) for each of the planktonic functional types (PFT) of the planktonic trophic network for the sampling stations evaluated and the average value of Total Phosphorus (TP) concentration (TP in mg.m^{-3} see Table 1) in these stations (Palacio-Betancourt, 2014) in the Riogrande II reservoir.

PFTs		**Biomass (ww mg m^{-3})**				
		Station 1 (pmf = 0.093) TP = 153	**Station 2 (pmf = 0.145) TP = 56**	**Station 4 (pmf = 0.177) TP = 36**	**Station 5 (pmf = 0.153) TP = 49**	**Station 7 (pmf = 0.144) TP = 58**
Cyclopoid	Observed	39.95	10.18	8.74	9.57	15.62
	Calculated	50.80	13.50	6.20	12.10	14.00
Asplanchna	Observed	782.95	165.67	251.26	182.60	525.13
	Calculated	906.60	191.00	120.50	164.50	198.90
Small cladocerans	Observed	3134.32	539.30	270.58	424.26	755.77
	Calculated	2800.00	824.00	461.30	690.90	862.80
Heterotrophic nanoflagellates	Observed					
	Calculated	16000.00	3700.00	2000.00	3100.00	3900.00
Heterotrophic Bacteria	Observed					
	Calculated	30000.00	7100.00	3800.00	5900.00	7500.00
Phytoplankton	Observed	15863.57	13851.31	19483.12	19013.61	40783.02
	Calculated	35000.00	8600.00	4600.00	7100.00	9000.00

pmf: prey meeting factor. Wet weight (ww).

the flows of the grazing chain were very low, therefore, the populations can no longer maintain themselves at the levels observed. Without the flows from the detritus, we would observe an abrupt decrease in the biomass and eventually some populations would reach the extinction limit. Therefore, the above arguments would support the idea in which the biomass of the phytoplankton that is not consumed and enters in the detritic path is sufficient for the detritivore to transfer this biomass and sustain the demand for food at higher trophic levels. These results agree with Sherr and Sherr (2002) which argue that much of the detritus is consumed by bacteria, and this microbial production is linked with higher trophic levels.

The values of the *pmf* in each simulation can be interpreted as the percentage of resources that the predator can access in certain concentrations of total phosphorus, ranging from 9.3 % to 17.7 %. Our results (Table 2) show that an increase in TP concentrations causes an increase in the biomass of the planktonic community, while the *pmf* values diminish. These results allow inferring that high densities of planktonic organisms, as well as detritus, could be affecting the *pmf* for predatory copepods. Cyclopoid species feed on plankton, are aggressive predators of protozoa, rotifers, and small aquatic animals (Hutchinson, 1967). Probably, this type of selective feeding can be affected by high concentrations of dissolved particles in water. Ramírez Restrepo *et al.* (2015) have indicated that in this tripton system (dead organisms, detritus, and colloidal substances of organic or inorganic origin) and non-phytoplankton is the component that contributes most to the attenuation of downward irradiation, which suggests a high concentration of detrital particles. In contrast to other predator-prey models, where the top predator regulates the population densities of its prey or the availability of resources regulates the densities of consumers, in these simulations, resources and consumers can control organisms at each trophic level of food webs, simultaneously.

In general, simple models predict that primary consumers would increase in the absence of higher predators. Danielsdottir *et al.* (2007) argued that the zooplankton biomass is determined by the interaction between the food quality and zooplanktivorous activity. In our model, we include the coupling between grazing and detrital chains to better predict the structure of the planktonic community. We found that only primary consumers (Small cladocerans) increase with enrichment, even in the presence of the top predator (Cyclopoid). This increase depends on other factors such as the probability of an encounter with the prey. It can be interpreted as the efficiency of the biomass transfer to the top predator is different for each station in the reservoir.

Filtration feed of small cladocerans and their strategies to avoid predation, in combination with the refuge effect that the environment can offer, can keep the abundance of predators at the biomass ranges observed (Villabona-González *et al.*, 2015). For instance, the feeding strategy of *Bosmina* dependent on the size of prey, allows this cladoceran to access resources such as autotrophic and heterotrophic nanoflagellates. Experimental results obtained by DeMott (1982) confirm the efficiency of this feeding strategy of *Bosmina* compared to other cladocerans of larger size.

Despite that biomass of H and B were not evaluated for the sampling period (2010 and 2013), the magnitude of calculated biomass for these PFTs seems to be mostly in the order of 10^4, being the H less abundant than B (Fig. 3, Table 2). Here, we represent a causal relationship between B and H via the dependence of H on its prey. Likewise, prokaryotes respond to the supply of organic material, derived from the death of phytoplankton and the unconsumed particulate material of zooplanktivorous (Sherr and Sherr, 2002).

The average simulated biomass for B and H was less than 16 000 and 30 000 mg m^{-3}, respectively (Table 2). We consider that these biomass values were relatively low since for the model we only considered the particulate organic carbon and not the dissolved carbon, product of algae and zooplankton excretion. Birge and Juday (1934) argue that in aquatic ecosystems the concentration of dissolved organic carbon can be 10 times greater than organic particulate carbon. We assume that detritus mineralization does not affect TP concentrations, which is not entirely true. These assumptions are often criticized in the literature because they ignore important aspects such as nutrient recycling. However, we include other aspects that are dynamically important in real trophic webs (and commonly ignored in other models) such as omnivory, detrital food chains, and energy flow from detrital channels to the highest trophic levels of the trophic network (Porter, 1996). The model presented here incorporates many of these characteristics that are difficult to take into account and, therefore, allows us the validation of previous predictions.

We assume 30 units of time (day) to reach the stability points of the system. During this period, the simulation of the biomass begins with the increase of the first levels of the trophic web (phytoplankton and detritus), followed by the main consumers of the detrital chain (B and H) (Fig. 3). On the other hand, the zooplankton biomass exhibits a decrease in the initial concentration at the early evolution, and gradually increases as the links with detrital chain are accounted for (Fig. 3). This behavior of the simulation is inherent to the feedback that occurs in the dynamic system and to the input values of the initial biomasses.

The traditional approaches to the study of food webs emphasize the transfer of productivity in the form of living organic plant matter through trophic levels. However, dead organic matter is often overlooked as a food resource that modifies habitat conditions for some organisms. We develop an integrating framework to understand the impact of detritus on the structure and dynamics of food webs through its influences on the stability and persistence of the system.

The confidence of our results is supported by the range of data observed for TP concentrations at each station, and also, for the biomass of each group included in the model for the photic zone of the Riogrande II reservoir. However, some flows of potential dynamic importance for the diet of many primary consumers (such as allochthonous flows of organic particulate matter) were not taken into account, and neither environmental factors (such as turbulence or hydraulic retention time), which are determinant in phytoplankton production.

CONCLUSIONS

The proposed model for the Riogrande II reservoir is validated in a range of total phosphorus concentrations that represents the spatial variability of the photic zone, including observations from several previous studies. The results of the simulations allow us to conclude that the magnitude of the biomass obtained in the studies carried out between 2010 and 2013 (Palacio-Baena *et al.*, 2013; Villabona-González, 2015; López-Muñoz, 2016) can be explained to a large extent by the causal relationships assumed in this model. We find that the main flows of the detrital food chain are determined by the interrelationship of the planktonic community of the photic zone in the reservoir. This effect is intensified by recognizing that this type of ecosystem generally receives additional amounts of organic matter from the basin, suggesting that dammed aquatic ecosystems are not only susceptible to enrichment by nutrients but also of organic matter. On the other hand, we include the hypothesis that biomass of top predators (Cyclopoids) is the result of the subsidized flows of the detrital food chain and the probability of an encounter of its prey, simultaneously. In correspondence, this model allows us to demonstrate that the dominance of *Bosmina* in the Riogrande II reservoir is due to its feeding strategy.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

Allee WC. Animal aggregations, a study in general sociology. Chicago: Univ. of Chicago Press; 1931. 452 p. Doi: https://doi.org/10.5962/bhl.title.7313

Berninger UG, Finlay BJ, Kuuppo-Leinikki, P. Protozoan control of bacterial abundances in freshwater. Limnol Oceanogr. 1991;36(1):139–147. Doi: https://doi.org/10.4319/lo.1991.36.1.0139

Berryman AA. The Origins and Evolution of Predator-Prey Theory. Ecology. 1992;73(5):1530–1535. Doi: https://doi.org/10.2307/1940005

Birge EA, Juday C. Particulate and dissolved organic matter in inland lakes. Ecol Monogr. 1934;4(4):440–474. Doi: https://doi.org/10.2307/1961650

Bloem J, Ellenbroek FM, Bär-Gilissen MJB, Cappenberg TE. Protozoan grazing and bacterial production in stratified Lake Vechten estimated with fluorescently labeled bacteria and by thymidine incorporation. Appl Environ Microbiol. 1989;55(7):1787–1795. Doi: https://doi.org/10.1128/AEM.55.7.1787-1795.1989

Chang KH, DOI H, Nishibe Y, Nakano SI. Feeding habits of omnivorous *Asplanchna*: comparison of diet composition among *Asplanchna herricki*, *A. priodonta* and *A. girodi* in pond ecosystems. J Limnol. 2010;69(2):209–216. Doi: https://doi.org/10.4081/jlimnol.2010.209

Christensen V, Pauly D. ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model. 1992; 61(3-4):169–185. Doi: https://doi.org/10.1016/0304-3800(92)90016-8

Danielsdottir MG, Brett MT, Arhonditsis GB. Phytoplankton food quality control of planktonic food web processes. Hydrobiologia. 2007; 589(1): 29–41. Doi: https://doi.org/10.1007/s10750-007-0714-6

Del Giorgio PA, Cole JJ. Bacterial growth efficiency in natural aquatic systems. Ann Rev Ecol Syst. 1998;29(1):503–541. Doi: https://doi.org/10.1146/annurev.ecolsys.29.1.503

DeMott WR. Feeding selectivities and relative ingestion rates of *Daphnia* and *Bosmina*. Limnol Oceanogr. 1982; 27(3): 518–527. Doi: https://doi.org/10.4319/lo.1982.27.3.0518

Estrada AL. Variacao espacial e temporal da comunidade zooplanctonica do reservatorio “La Fe”, Antioquia, Colombia (tesis de maestría). Sao Paulo: Universidad de Sao Paulo; 1999. 78 p.

Giraldo M. Composición de la dieta del rotífero *Asplanchna girodi* (De Guerne, 1888) y su variación temporal y espacial en el embalse Riogrande II (Antioquia, Colombia) (trabajo de grado). Medellín: Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia; 2010. 80 p.

Hakspiel-Segura C, Canosa-Torrado A, Niño-García JP. Variación espacial y temporal del bacterioplancton en un reservorio de alta montaña en los Andes colombianos. Hidrobiológica. 2015;25(1): 62–73.

Hutchinson GE. A Treatise on Limnology: Introduction to Lake Biology and the Limnoplakton. New York-London-Sydney: John Wiley; 1967. 1115 p.

Jørgensen SE, Bendoricchio G. Fundamentals of ecological modelling. USA: Elsevier B.V; 2011. 530 p.

López-Muñoz MT. Aspectos taxonómicos y ecológicos del fitoplancton eucariótico del embalse Riogrande II (Antioquia, Colombia) (tesis de doctorado). Medellin: Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia; 2016.

López-Muñoz MT, Ramírez-Restrepo JJ, Palacio-Baena JA, Echenique RO, De Mattos-Bicudo CE, Parra-García EA. Biomasa del fitoplancton eucariota y su disponibilidad para la red trófica del embalse Riogrande II (Antioquia, Colombia). Rev Acad Colomb Ci Exact Fís Nat. 2016;40(155):244–253. Doi: https://doi.org/10.18257/raccefyn.336

Margalef R. Limnología. Barcelona: Ediciones Omega, S.A; 1983. 1010 p. Doi: https://doi.org/10.4319/lo.1984.29.6.1349b

Marten GG, Reid JW. Cyclopoid copepods. J Am Mosq Contr Ass. 2007;23(sp2):65–92. Doi: https://doi.org/10.2987/8756-971X(2007)23[65:CC]2.0.CO;2

Matz C, Boenigk J, Arndt H, Jürgens K. Role of bacterial phenotypic traits in selective feeding of the heterotrophic nanoflagellate *Spumella* sp. Aqua Micro Ecol. 2002;27(2): 137–148. Doi: https://doi.org/10.3354/ame027137

Moore JC, Berlow EL, Coleman DC, Ruiter PC, Dong Q, Hastings A, *et al*. Detritus, trophic dynamics and biodiversity. Ecol Lett. 2004;7(7):584–600. Doi: http://doi.org/10.1111/j.1461-0248.2004.00606.x

Munkittrick KR, McCarty LS. An integrated approach to ecosystem health management: top-down, bottom-up or middle-out? Aqua Ecos Health. 1995; 4: 77–90. Doi: https://doi.org/10.1007/BF00044791

Odum E, Barrett G. Fundamentos de Ecología. 5 ed. México: International Thomson Editores; 2006. 598 p.

Palacio-Baena J, Herrera-Loaiza N, López-Muñoz M, Palacio-Betancourt H, Rodríguez M. Limnoecología de los embalses Riogrande II, La Fe y Porce II. En: Estudio de la problemática ambiental de tres embalses de empresas públicas de Medellín ESP para la gestión integral y adecuada del recurso hídrico. Medellín: Universidad de Antioquia; 2013.

Palacio-Betancourt HM. Dinámica espacio-temporal de las cianobacterias en el embalse Riogrande II (tesis de doctorado). Medellín: Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia; 2014.

Parra-García EA, Rivera-Parra N, Picazo A, Camacho A. Detrital food chain as a possible mechanism to support the trophic structure of the planktonic community in the photic zone of a tropical reservoir. Limnetica. 2020;39(1):511-524. Doi: https://doi.org/10.23818/limn.39.33

Peters RH. The role of prediction in limnology. Limnol Oceanogr. 1986;31(5):1143–1159. Doi: https://doi.org/10.4319/lo.1986.31.5.1143

Polovina J. ECOPATH. A User’s Manual and Programs Listing. National. NOAA, Honolulu Adm: Marine Fisheries Service; 1983.

Porter KG. Integrating the microbial loop and the classic food chain into a realistic planktonic food web. En: Polis GA, Winemiller KO. Food Webs. Boston, MA: Springer; 1996: 51-59. Doi: https://doi.org/10.1007/978-1-4615-7007-3_5

Ramírez Restrepo J, Arcila L MC, Sepúlveda A SC. Cuantificación de los componentes que afectan el coeficiente de atenuación vertical para irradiancia descendente en el embalse Riogrande II (Colombia). Rev Acad Colomb Ci Exact Fís Nat. 2015; 39(151): 228–238. Doi: https://doi.org/10.18257/raccefyn.150

Restano AML, Ramírez Restrepo JJ, Echenique RO, Vallejo AA, Ortiz LYM. Dinámica espacio-temporal de cuatro especies de *Staurastrum* (Meyen 1829, emend. Ralfs 1848) en un embalse eutrófico colombiano. Oecol Australis. 2011;15(3):726–746. Doi: https://doi.org/10.4257/oeco.2011.1503.22

Sherr EB, Sherr BF. Significance of predation by protists in aquatic microbial food webs. ALJMAO. 2002;81(1–4): 293–308. Doi: https://doi.org/10.1023/A:1020591307260

Toledo AP, Talarico M, Chinez SJ, Agudo EG. A aplicação de modelos simplificados para a avaliação de procesos de eutrofização em lagos e reservatórios tropicais. Camboriú, Brasil: XIX Congreso interamericano de Engenharia e ambiental; 1983. p. 57.

Villabona-González SL. Relaciones ecológicas de la biomasa de las poblaciones de rotíferos y microcrustáceos en la zona fótica del embalse Riogrande II, Antioquia, Colombia (tesis de doctorado). Medellin: Instituto de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Antioquia; 2015. 131 p.

Villabona-González SL, Buitrago-Amariles RF, Ramírez-Restrepo JJ, Palacio-Baena JA. Biomasa de rotíferos de dos embalses con diferentes estados tróficos (Antioquia, Colombia) y su relación con algunas variables limnológicas and its relationship with some limnological variables. Actual Biol. 2014;36(101):149–162.

Villabona-González SL, Ramírez-Restrepo JJ, Palacio-Baena JA, Bonecker CC. Respuesta de la biomasa zooplanctónica a los gradientes de estado trófico y precipitación de un embalse tropical. Rev Acad Colomb Ci Exact Fís Nat. 2015; 39(152): 374–388. Doi: https://doi.org/10.18257/raccefyn.203

Walline PD, Pisanty S, Gophen M, Berman T. The ecosystem of Lake Kinneret, Israel. In Trophic models of aquatic ecosystems. Manila, Philippines: ICLARM Conference Proceedings. 1993;26: 103–109.

Weisse T. The annual cycle of heterotrophic freshwater nanoflagellates: role of bottom-up versus top-down control. J Plank Res. 1991; 13(1): 167–185. Doi: https://doi.org/10.1093/plankt/13.1.167

Wetzel R. Limnology: lake and river ecosystems. 3 ed. San Diego (CA): Academic Press; 2001. 1006 p.