



## THE ROLE OF HABITAT COUPLING BY ZOOPLANKTON DRIVING POPULATION DYNAMICS AND STABILITY IN SHALLOW LAKES

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**Abstract:** Studies of population stability in shallow lakes are yet to explain how fishless ponds, with high algae productivity, can have stable zooplankton-algae populations throughout the year. These studies have traditionally overlooked the role of benthic-pelagic coupling, a phenomenon that has noticeable effects on population stability in aquatic environments. We analyzed a simple model to show that benthic-pelagic habitat coupling can explain discrepancies between the behavior of classical predator-prey models and the patterns observed in natural aquatic systems. We used a Lotka-Volterra type model of zooplankton and algae, explicitly modeled as phytoplankton and periphyton. Zooplankton could eat in both algal compartments, presenting a multi-chain omnivore configuration, whereas phytoplankton and periphyton engage in exploitative competition as system support capacity increases. We also modeled the algal exchange among compartments. Our model results show that (1) zooplankton—algae systems tend to be stable up to high nutrient values at intermediate degrees of omnivory, that (2) algae exchange among compartments may dampen stability and that (3) exploratory competition between phytoplankton and the periphyton can also decrease stability. The model results are supported by empirical results available in the literature. Despite the limitations of the modeling approach, our results emphasize the role of habitat coupling and contribute to deepening the understanding of the processes and mechanisms capable of promoting the stability of population dynamics in shallow lakes.

**Keywords:** Omnivory, Zooplankton, Phytoplankton, Periphyton, Mathematical modeling.

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### INTRODUCTION

Population stability is an important metric that can inform about populations in danger

of local extinction. This measure can be summarized as the variation of the number of individuals in a population over time (Grimm & Wissel 1996). Although it seems like a simple

concept, its definition and measurement in an effective way prove to be extremely complex. Several elucidations have been proposed for this concept, the most applied to be those that involve the relative variability of a population as a function of space and/or time (Grimm *et al.* 1992, Bodin & Wiman 2004). However, the limits of these spatial and/or temporal parameters are not usually well defined and the collection of the necessary data over time can be an extremely difficult task and, therefore, rarely sufficient (Paine 1969, Grimm & Wissel 1996). Despite the difficulties, the concept of population stability remains extremely important for ecology and conservation, acting as a key determinant part in the distinction between natural stochastic variations and the ecosystem responses to anthropic environmental changes (Yang *et al.* 2019).

One of the first well-defined concepts about Population Ecology was the development of dense-dependent models that relate the size of a population to the carrying capacity of the environment (Lotka 1925). Another relevant aspect of population dynamics for this work is the theory of alternative stable states, which predicts that ecosystems may exist in multiple equilibrium states characterized by unique combinations of biotic and abiotic conditions (Beisner *et al.* 2003), consequently, population stability may vary during the shift between different states (Scheffer *et al.* 2001). Several mechanisms capable of stabilizing or destabilizing populations are known. One of these mechanisms that have been gaining importance is omnivory. It is very common for animals to feed on resources from alternative food chains, often beyond the limits of the habitat in which the animal is commonly found. Such organisms, capable of acquiring food in different habitats, are classified as multi-chain omnivores (Polis & Strong 1996, Vadeboncoeur *et al.* 2005). Multi-chain omnivory is a form of habitat coupling that is relatively common in aquatic ecosystems and its implications are yet to be properly understood (Schindler & Scheuerell 2002, Liu *et al.* 2020).

There is a controversial debate among ecologists about the ability of multi-chain omnivory to stabilize or destabilize population

dynamics. Some studies point to the hypothesis that omnivorous predators have the competence to maintain high populations even when there is a decrease in the abundance of a certain prey (McCann & Hastings 1997). This prey, therefore, will be at greater risk of local extinction due to the fact that it's in a habitat with a high density of its predator (Pimm 1978, Vanni *et al.* 2005). Nonetheless, the idea that population stability is directly proportional to the number of energy pathways, or connections in the trophic webs that characterize any community is an axiom accepted by some ecologists (MacArthur 1955, Paine 1969), and rejected by others (May 1974, Jacquet *et al.* 2016). Populations of planktonic herbivores, for example, are known for their tendency to oscillate over time as a consequence of the exacerbated consumption of algae (Rose *et al.* 1988). These oscillations are observed in both zooplankton and phytoplankton populations and can be represented by Lotka-Volterra equations. Such models, generally, have a stable balance (without oscillatory behavior) when algae productivity is low (Scheffer 1991). However, an increase in productivity can lead to the paradox of enrichment, causing ever greater population fluctuations as algae productivity increases (Rosenzweig 1971). These oscillations can become so large that both algae and zooplankton populations can become locally extinct (Scheffer 1991). Despite the mentioned models predicting unstable population dynamics when algae productivity is high, there are records of stable algae-zooplankton population dynamics, or persistent populations, even in natural environments with high algae productivity (De Boer & Scheffer 1995, Vadeboncoeur *et al.* 2005, Hobbs *et al.* 2014).

Some factors have been considered keys to stabilizing population dynamics in aquatic ecosystems, such as the presence of large amounts of inedible algae (Kretzschmar *et al.* 1993) the top-down effect of zooplanktivorous fish (Scheffer 1991), and some others (Vadeboncoeur *et al.* 2005). Yet, stable balances of these populations are observed in nature even in high-productivity lakes, without zooplankton predators and the presence of large amounts of inedible algae (Scheffer & van Nes 2007, Lancelotti *et al.* 2009, De Kluijver *et al.* 2015) and there is still no clear

consensus on the mechanisms that maintain this stability. Therefore, it is important to investigate which factors affect the population dynamics of these lakes without zooplankton predators and relative high algae productivity.

In addition, many studies on this subject neglect the role that benthic communities have in lake ecosystems and focus mostly on the pelagic habitat. However, the benthic-pelagic coupling can have strong effects on population dynamics, especially on shallow lakes (Rivera Vasconcelos *et al.* 2018, Wang *et al.* 2019, Liu *et al.* 2020). In fact, field experiments and observations in shallow lakes show that zooplankton species are fully capable of multi-chain omnivory, being able to feed directly on microbial mats from benthic producers and even be directly supported by them through the resuspension due to the mixture of water caused mainly by the wind (Vadeboncoeur *et al.* 2005, Hudjetz *et al.* 2008, De Kluijver *et al.* 2015). This benthic production, of which zooplanktonic organisms are capable of feeding, consists of periphytic algae. Periphyton means a microbiota community made up of algae, bacteria, fungi, animals, and organic and inorganic debris that are attached to submerged organic or inorganic substrates, living or dead, which acts as a primary producer (Ferragut 2010). Periphytic algal communities are more developed in clear and shallow water bodies as sunlight is able to reach the benthic region. This implies a competitive relation for light between phytoplankton and periphytic algae, as an increase in the pelagic algae concentrations makes the water column more turbid and reduces the amount of sunlight capable of reaching the benthic region, leading to reduced periphyton biomass (Devlin *et al.* 2015, Vasconcelos *et al.* 2016, Rivera Vasconcelos *et al.* 2018). Both sunlight attenuation and resuspension of periphytic algae caused by wind are forms of habitat coupling that may have noticeable consequences for population dynamics (Tunney *et al.* 2018).

We investigated how the benthic-pelagic coupling affects the population dynamics of benthic and pelagic organisms in a hypothetical fishless shallow lake. To this end, we have modeled a three-species food web composed of two producers, phytoplankton and periphyton, and a top predator, zooplankton, with the

capacity to choose between different prey based on the relative abundance of each one. We also incorporate in the model two more forms of benthic-pelagic coupling that have relevant effects on the population dynamics of shallow lakes: the resuspension of periphyton caused by the wind and the competition for sunlight between phytoplankton and periphytic algae (Devlin *et al.* 2015, Vasconcelos *et al.* 2016, Rivera Vasconcelos *et al.* 2018, Tunney *et al.* 2018). To do this, we adapt the classical algae-zooplankton models made by Scheffer (1991), removing the presence of fish and adding the periphytic algae as an alternative food source. We also incorporated a prey preference variable, which allows us to regulate the intensity of the multi-chain omnivory by zooplankton. Our goal was to evaluate how the benthic-pelagic coupling will affect the population dynamics, particularly, its effect on population stability.

## MATERIAL AND METHODS

### *Model formulation*

Scheffer (1991), based on the works of Holling (1959), Lotka (1925) and Rose *et al.* (1988), proposed a system of first-order ordinary differential equations to simulate algae-zooplankton population dynamics, such as:

$$\frac{dPP}{dt} = r_{PP}PP \left(1 - \frac{PP}{Kt}\right) - g_z PP Z \frac{PP}{PP + h_{PP}} \quad (1)$$

$$\frac{dZ}{dt} = e_z g_z Z \frac{PP}{PP + h_{PP}} - m_z Z \quad (2)$$

, in which PP = Algae biomass (mg/L), r = Maximum growth rate of phytoplankton (day<sup>-1</sup>), K = Carrying capacity (mg/L), g<sub>z</sub> = Maximum grazing rate of zooplankton on algae (day<sup>-1</sup>), h<sub>pp</sub> = Monod's saturation constant (mg/L), Z = Zooplankton biomass (mg/L), e<sub>z</sub> = Prey assimilation efficiency of zooplankton, m<sub>z</sub> = Rate of zooplankton mortality and respiration (day<sup>-1</sup>).

To add the multiple-chain omnivory to the simulation, it was necessary to break equation (1) into two, one for the phytoplankton (pelagic food source) and the other for the periphyton (benthic food source). Also, terms that represent the intensity of the zooplankton omnivory and the transport of periphyton biomass from the benthic to the pelagic environment due to the movement of the water body were added. Another important

process that was included in the model was the shading of the benthic region (light attenuation) caused by phytoplankton. A representative diagram of the food web to be studied is shown in figure 1.

The inclusion of the multi-chain omnivory was done according to Post *et al.* (2000). As zooplankton is able to feed in both pelagic and benthic zone (Hudjetz *et al.* 2008, De Kluijver *et al.* 2015), two variables,  $\delta_{pp}$ , and  $\delta_{pb}$ , multiply the terms referring to zooplankton feeding. These parameters are called prey preference variables and they ranged from 0 to 1, in which:  $\delta_{pp} + \delta_{pb} = 1$ . They function as percentages of preference for one food source over the other.

The equations for the  $\delta_{pp}$  e  $\delta_{pb}$  factors are below:

$$\delta_{pp} = \frac{\pi PP}{\pi PP + (1 - \pi)PB} \quad (3)$$

$$\delta_{pb} = \frac{(1 - \pi)PB}{\pi PP + (1 - \pi)PB} \quad (4)$$

By varying  $\pi$ , present in both equations above, we can regulate, and therefore study, the intensity

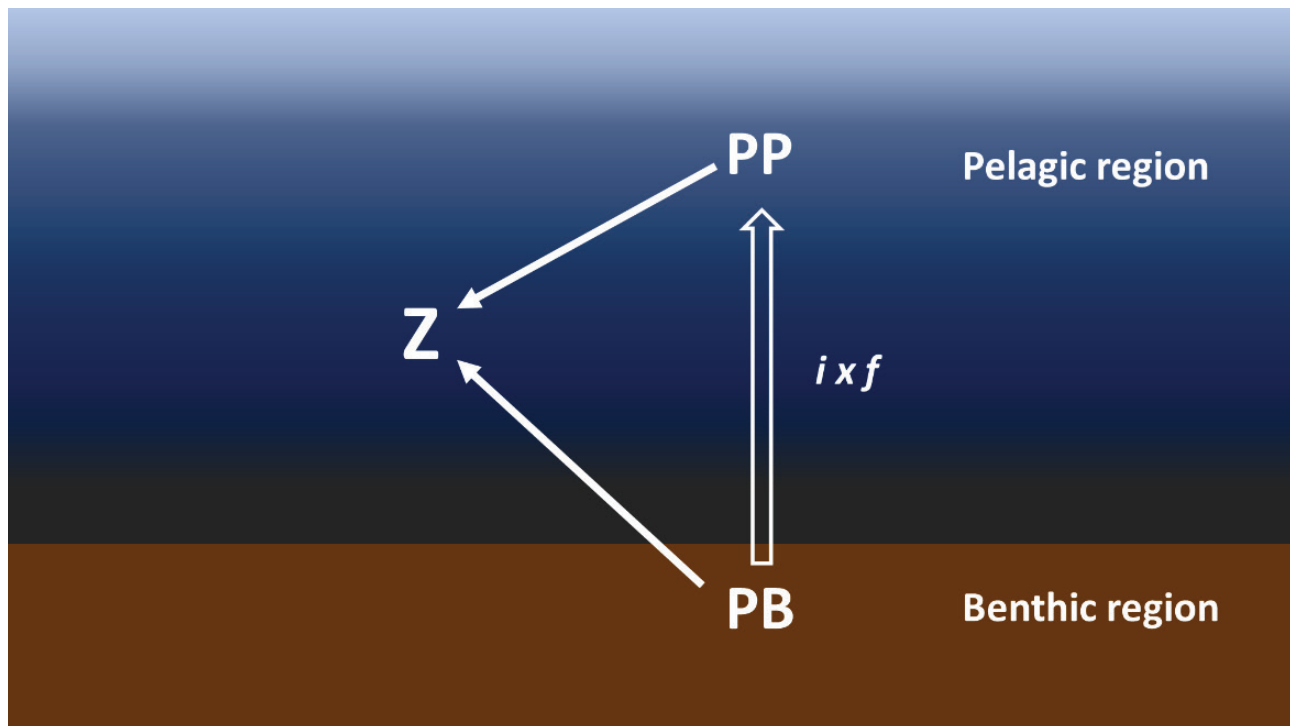
and the consequences of the omnivorous behavior.

The amount of light that reaches the benthic region and is available for photosynthesis of the periphyton is a function of the phytoplankton concentration. This phenomenon was included in the model through the variable  $p$ , which is directly proportional to the phytoplankton concentration. This variable multiplies the carrying capacity in the term referring to the growth of phytoplankton and  $(1 - p)$  multiplies the carrying capacity in the term referring to the growth of the periphyton. This implies that as the phytoplankton concentration increases and the water column becomes more turbid, less sunlight reaches the benthic region, then, the proportion of the carrying capacity available to the phytoplankton increases and that of the periphyton decreases.

The calculation of  $p$  was done accordingly to that of Devlin *et al.* (2015).

$$bp = 1 - mxp \quad (5)$$

$$p = mxp - \frac{(mxp - bp)}{e^{K \cdot \theta}} \quad (6)$$



**Figure 1.** Spatial configuration of the model. Zooplankton (Z) is able to feed on both phytoplankton (PP) and peripheryton (PB). Despite the prey being confined in their environments, there is a contribution of biomass, due to the movement of the water column, from the periphyton to the phytoplankton, represented by the unfilled arrow. The color gradient in the pelagic zone represents the attenuation of the available light in the water column as the depth increases. The greater the abundance of phytoplankton, the greater the attenuation of light.

Where  $b_p$  is the minimum proportion of the carrying capacity attributed to benthic production,  $m_{xp}$  is the maximum proportion of the carrying capacity attributed to pelagic production,  $K$  is the carrying capacity (mg/L), and  $\theta$  is the scattering angle coefficient of the incident light beam in the water.

At last, we modeled the contribution of algal biomass from the benthic zone to the pelagic zone due to the mixture of the water column caused mainly by the wind. Being  $f$  the proportion of benthic algal forms susceptible to removal by the water movement and  $i$  being the daily mixing rate of the water mass, by multiplying the terms  $f$ ,  $i$ , and  $PB$  (periphyton concentration) we have the biomass of benthic algae that goes to the pelagic zone per day and becomes available to zooplankton consumption in that region. This term was subtracted from the periphyton equation and added to the zooplankton equation as another food source available in the pelagic zone.

Including all the considerations above in the model, we have:

$$\frac{dPP}{dt} = r_{PP}PP \left(1 - \frac{PP}{Kt \cdot p}\right) - \delta_{PP}g_{zPP}Z \frac{PP}{PP + h_{PP}} \quad (7)$$

$$\frac{dPB}{dt} = r_{PB}PB \left(1 - \frac{PB}{Kt(1-p)}\right) - \delta_{PB}g_{zPB}Z \frac{PB}{PB + h_{PB}} - ifPB \quad (8)$$

$$\begin{aligned} \frac{dZ}{dt} &= \delta_{PP} \cdot e_z \cdot g_{zPP} \cdot Z \frac{PP}{PP + h_{PP}} + \delta_{PB} \cdot e_z \cdot g_{zPB} \\ &\cdot Z \frac{PB}{PB + h_{PB}} + \delta_{PP} \cdot e_z \cdot g_{zPB} \cdot Z \frac{ifPB}{ifPB + h_{PB}} - m_z Z \end{aligned} \quad (9)$$

The terms  $PP$  and  $PB$  refer to the phytoplankton and the periphyton, respectively. All the variables used in the model with their respective assigned values can be found in the online supplementary material. These values were based on Scheffer (1991) and Rose *et al.* (1988).

### Numerical analysis

The software R (R Core Team 2020) was used to perform the simulations. To run the system of first-order differential equations, we use the *deSolve* package (Woodrow 2010) which is specific for this type of analysis. The *ggplot2* (Wickram 2016) and *ggpubr* (Kassambara 2020) packages were used to represent the results graphically. To study how the variation of parameters: intensity of omnivory

( $\pi$ ), mixing rate of water mass ( $i$ ) and intensity of competition for light ( $m_{xp}$ ) affect population stability, bifurcation diagrams were generated for four values of  $\pi$ , four values of  $i$  and two values of  $m_{xp}$ , totalizing 32 (4 x 4 x 2) different sets of conditions and, as there are three organisms, 96 (32 x 3) bifurcations diagrams.

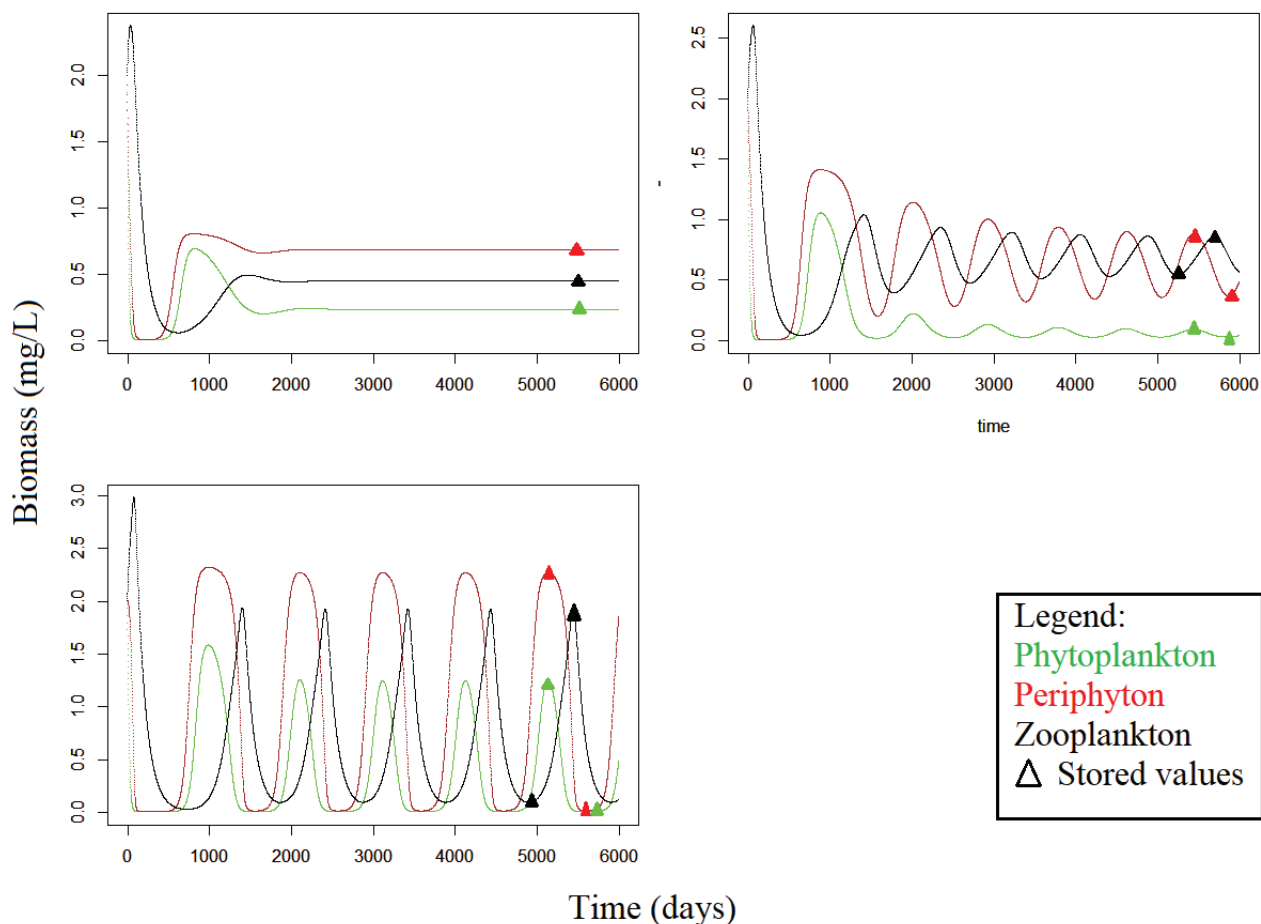
In order to quantify and compare the population stability, the bifurcation diagrams were generated along with a range of the algal carrying capacity of the lake (x-axis). As the main cause of the oscillations is the excessive consumption of algae due to high algae densities in conditions of high carrying capacity (Rose *et al.* 1988, Scheffer 1991), we observe what is the maximum carrying capacity that maintains population dynamics stable (without oscillatory behavior) for each of the 32 sets of conditions. By observing which scenarios have stable population dynamics over a longer range of carrying capacity, we can see how the studied parameters influence the population stability by comparing the carrying capacity ( $K$ ) value at which the oscillations begin. The x-axis value at which the system changes from a stable to an oscillatory behavior is called Hopf bifurcation point, identified below in this work as  $b_h$ . The higher the carrying capacity at which the oscillations begin ( $b_h$ ), the more robust the system's stability. Although there are 96 different bifurcation diagrams in total, we can only observe 32 different Hopf bifurcation points because, for each set of conditions, oscillations began at the exact same value of  $b_h$  for all the three organisms (figure 3). So, even though there are three bifurcation diagrams for every one of the 32 sets of conditions, the  $b_h$  values of these three diagrams will always be the same.

We choose to generate only 96 bifurcation diagrams, and consequently 32 values of  $b_h$ , because the values of the Hopf bifurcation points ( $b_h$ ), in which the simulation changes from stable ( $dPP/dt = dPB/dt = dZ/dt = 0$ ) to periodic oscillatory ( $[dPP/dt; dPB/dt; dZ/dt] \neq 0$ ) are exact mathematical results, there is no variation associated to them. So, in this experiment, as there is no statistical error associated with the generated values, we only had to have enough data to observe how the predictor variables ( $i$ ,  $\pi$  and  $m_{xp}$ ) would relate to the dependent variable ( $b_h$ ).

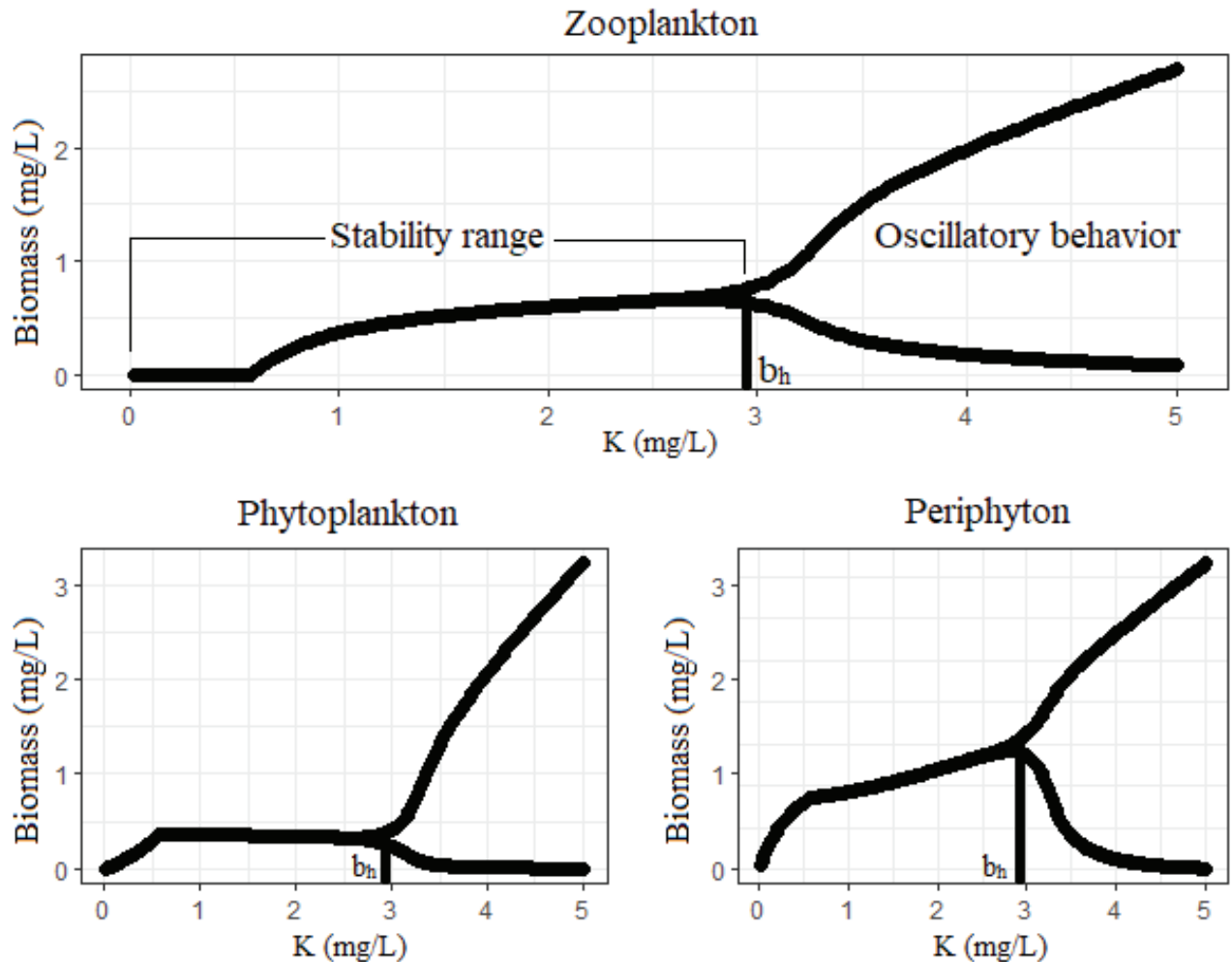
And, we can be sure that the dependent variable ( $b_h$ ) will behave as a predictable continuous mathematical function, as it is just the result of a change in the Hopf bifurcation point of a system of predictable continuous mathematical functions in the studied interval [0.25; 1.00], as package deSolve (Woodrow 2010) warns the user about any discontinuities in the simulation. Also, we can graphically see all necessary the predictable behaviors in figures 2 and 3. Therefore, we don't need to run the simulation a lot of times to know what's going to be the relation between a particular predictor variable and the dependent variable. That's why we only ran the simulation for four values of mixing rate of water mass ( $i$ ) and intensity of omnivory ( $\pi$ ). We can be sure that there won't be any unexpected behavior between these four values.

## RESULTS

All the bifurcation diagrams generated by the simulations are consistent with classic results from other modeling studies of population dynamics in shallow lakes, in which the algal density grows as a function of the carrying capacity (with only one y-axis value for each x-axis value) at relatively low carrying capacity values. Eventually, the Hopf bifurcation point ( $b_h$ ) occurs and the values of maximum and minimum begin to distinguish themselves. Once this happens, the difference between these values (amplitude of the oscillation) only grows as carrying capacity increases, which causes ever greater population fluctuations, leading to a decrease in the values of local minimum and an increase in the local risk of extinction. It was observed that the carrying capacity values of the Hopf bifurcation points



**Figure 2.** Zooplankton, phytoplankton and periphyton biomass concentrations as a function of time, simulated for conditions with a) low (1.0 mg/L), b) medium (3.5 mg/L) and c) high (5.0 mg/L) values of carrying capacity. The triangle symbols indicate the maximum and minimum stored values of biomass. As carrying capacity grows, population stability decreases. In (a), the carrying capacity is not big enough to cause oscillations, so population dynamics are stable, in (b) there are small oscillations and in (c) the oscillations are bigger.



**Figure 3.** Bifurcation diagrams of the maximum and minimum values of biomass obtained over an interval of carrying capacity (0.0 - 5.0) mg/L. It is noticed that the three populations present stability up to approximately 3.0 mg/L (Hopf bifurcation point) of carrying capacity, where the maximum and minimum values of biomass are the same, as shown in figure 2 (a). After that, the oscillations begin and the maximum and minimum values of biomass start to differentiate. After 3.0 mg/L, the system switches from a stable to an unstable behavior, as also shown in figure 2 (b) and (c).

decreased as the mixing rate of water mass increased (Tables 1 and 2). Comparing the  $b_h$  values of the columns of tables 1 and 2, where all the variables are the same, and we vary only mixing rate of water mass, the highest values for  $b_h$  were obtained for  $i = 0.25$  and the lowest values for  $i = 1.00$ , for all the columns of both tables, indicating a possible destabilizing effect of the mixing rate of water mass on population dynamics.

In regards to the intensity of omnivory ( $\pi$ ), for the condition of low competition for light (Table 1), the highest values of  $b_h$  were obtained at  $\pi = 0.90$  and for the condition of high competition for light (Table 2), at  $\pi = 0.75$ , suggesting that greater

intensity of omnivory is needed to maintain stability as less light reaches the benthic region. Also, no direct or inverse relation between  $\pi$  and  $b_h$  was observed, stability increases with the intensity of omnivory until a maximum value ( $\pi = 0.90$  for the low competition for light and  $\pi = 0.75$  for the high competition for light), then  $b_h$  starts to decrease as  $\pi$  increases. The smallest stability intervals were obtained for the conditions with no multi-chain omnivory ( $\pi = 1.00$ ), in which the zooplankton only feeds on phytoplankton (Tables 1 and 2), highlighting the stability effect of the multi-chain omnivory.

Comparing the conditions of low and high

competition for light, the median and the interquartile range of the 16 values of carrying capacity in which the oscillations begin ( $b_h$ ) was  $Mb = 2.75$  mg/L and  $IQR = 1.25$  mg/L for the scenario with low competition for light (Table 1) and  $Mb = 2.20$  mg/L and  $IQR = 0.7$  mg/L for the scenario with high competition for light (Table 2), which represents a 25% increase in the median value. Furthermore, comparing all the corresponding  $b_h$  values between the conditions of low and high competition for light (Tables 1 and 2), we could see that the stability range is always greater for the condition of low competition for light.

### DISCUSSION

In view of the diverse biotic and abiotic relationships that make up ecosystems, the analysis of natural processes is often unfeasible due to the great difficulty in isolating variables and studying their causes and effects separately over the period of time assumed as necessary (Paine 1969, Grimm & Wissel 1996). The modeling of trophic relations in ecology, despite being a huge

simplification of reality, works as a complement to the direct study of natural ecosystems, allowing the manipulation of ecological processes over time with relative ease. However, if a model predicts that a particular food web is unstable, for example, its interpretation can be complicated due to the intrinsic differences that the model will present from complex natural systems (Vadeboncoeur *et al.* 2005). Even so, many elements of the model proposed in this work are consistent with patterns observed in real lakes and, despite the limitations, our results were consistent with those of direct studies of natural lake ecosystems. (Hobbs *et al.* 2014, De Kluijver *et al.* 2015, Devlin *et al.* 2015, Wang *et al.* 2019). Our model predicts that the multi-chain omnivory by zooplankton can be one of the reasons that explain how many lakes in tropical coastal regions, especially small fishless lakes with intense maritime influence and high algal productivity, have stable zooplankton populations throughout the year (Scheffer & van Nes 2007, Lancelotti *et al.* 2009). These lakes are particularly shallow, which allows the development of a vast periphyton community

**Table 1.** Values of carrying capacity (mg/L) in which the Hopf bifurcation point ( $b_h$ ) occurred, and the system switched from a stable to an periodic oscillatory behaviour. These values were generated for four different conditions of intensity of omnivory ( $\pi$ ), four different conditions of mixing rate of water mass ( $i$ ) and for a low competition for light environment ( $mpx = 0.60$ ). The arrows point in the direction in which the values of  $b_h$ , and hence stability, increases.

Mixing rate of water mass	Intensity of Omnivory			
	$\pi = 0.50$	$\pi = 0.75$	$\pi = 0.90$	$\pi = 1.00$
$i = 0.25$	2.6	3.2	4.4	2.0
$i = 0.50$	2.6	3.1	4.1	1.9
$i = 0.75$	2.5	2.9	3.9	1.8
$i = 1.00$	2.5	2.9	3.8	1.7

**Table 2.** Values of carrying capacity (mg/L) in which the Hopf bifurcation point ( $b_h$ ) occurred, and the system switched from a stable to an periodic oscillatory behaviour. These values were generated for four different conditions of intensity of omnivory ( $\pi$ ), four different conditions of mixing rate of water mass ( $i$ ) and for a high competition for light environment ( $mpx = 0.80$ ). The arrows point in the direction in which the values of  $b_h$ , and hence stability, increases.

Mixing rate of water mass	Intensity of Omnivory			
	$\pi = 0.50$	$\pi = 0.75$	$\pi = 0.90$	$\pi = 1.00$
$i = 0.25$	2.5	2.9	2.1	1.6
$i = 0.50$	2.4	2.7	2.0	1.6
$i = 0.75$	2.4	2.6	1.9	1.5
$i = 1.00$	2.3	2.4	1.9	1.4



that can serve as food for zooplankton, in addition, the reduced depth approximates the pelagic and benthic habitats.

The axiom that population stability is directly proportional to the number of connections in the trophic webs (MacArthur 1955, Paine 1969) was corroborated by our results. The most unstable scenarios (lower  $b_h$  values), in all cases, were obtained for simulations without the omnivorous behavior of zooplankton ( $\pi = 1.00$ ). However, it is necessary to emphasize that, to reach this result, we compare different scenarios of a simple food web composed by only two trophic levels and three organisms. Such a result is expected if we compare the population stability of a condition with no multi-chain omnivory, where the herbivore can only consume one producer, with another condition where the herbivore can consume two producers, in which the prey preference variables,  $\delta_{pp}$  e  $\delta_{pb}$ , limit the consumption of a given producer when its biomass is relatively smaller than that of the other, mitigating the decrease in its population density and attenuating oscillations Post *et al.* (2000).

Although the lowest  $b_h$  values were obtained for conditions without multi-chain omnivory, the highest  $b_h$  values were not obtained for conditions with maximum omnivory ( $\pi = 0.50$ ), but for intermediate values of omnivory intensity ( $0.50 < \pi < 1.00$ ), suggesting a trade-off in such relationship. This happens because the excessive consumption of algae can lead to the paradox of enrichment and generate even greater population oscillations (Scheffer 1991, Alebraheem 2020). However, the conditions of high intensity of omnivory ( $\pi \approx 0.50$ ) are the ones that maximize algae consumption and, consequently, also maximize the risk of the paradox of enrichment. Despite the prey preference variables mitigating the population decline of the scarcest food source, the growth of zooplankton may be high enough when  $\pi \approx 0.50$ , as it has full access to both sources of food, that this mitigation is not sufficient to prevent the excessive algae consumption and the subsequent fast decrease in both algae populations. Therefore, intermediate values of intensity of omnivory, in which zooplankton prefers to feed on phytoplankton over periphyton, are the ones that present the most stable population dynamics. In these values, the population densities of the food sources are

still stabilized by the prey preference variables. However, the omnivory is not intense enough to result in the excessive growth of zooplankton and in the paradox of enrichment. This result is consistent with studies that quantified the origin of zooplankton diets and showed that, even under conditions in which the periphyton is abundant, zooplankton has a feeding preference for phytoplankton and generally only consumes periphyton when pelagic algae biomass is scarce (Hudjetz *et al.* 2008, De Kluijver *et al.* 2015). Mccann (2000) also found that intermediate levels of omnivory promote stability in a three-species food chain modeled by differential equations.

It is interesting to notice that there was an increase in the intensity of the optimal omnivory (the value of  $\pi$  that resulted in the highest value of  $b_h$ ) from the condition of low competition for light to the condition of high competition for light. As the periphyton biomass decreased in the condition with high competition for light, the intensity of the optimum omnivory (*i.e.*, that prevents oscillations) had to increase in order to compensate for this reduction. Furthermore, if we compare the  $b_h$  values of the two conditions of competition for light, the stability intervals are greater (25% increase in the median value) for simulations with low competition for light and, consequently, a larger periphyton biomass. The mixing rate of water mass ( $i$ ), which causes resuspension and can reduce the amount of periphyton standing stock, presented a negative effect on the stability of the population dynamics. In agreement, studies have shown that the attenuation of resuspension can restore turbid shallow lakes to an alternative stable clear-water state with greater benthic communities (Scheffer *et al.* 2003, Roozen *et al.* 2007). This suggests that the larger the periphytic algal communities or the more developed the benthic region, the more robust the lake's population stability will be. This result was also observed in natural conditions by several researchers (*e.g.* Jones & Waldron 2003, Hobbs *et al.* 2014, De Kluijver *et al.* 2015) and in the modeling of lake's trophic relationships by Vadeboncoeur *et al.* (2005), in which the authors simulated trophic webs of lake ecosystems and concluded that the multi-chain omnivore better stabilizes population dynamics when both periphyton and phytoplankton contribute

substantially to primary production. All of these results point out to the fact that the role of benthic communities in ecosystems must be taken into account when management laws and practices are made.

We speculate that, despite the existence of a well-developed periphytic algal community in a given lake, the paradox of the enrichment effect may not occur due to the fact that zooplankton is mostly a pelagic organism (Schindler & Scheuerell 2002, Vadeboncoeur *et al.* 2005) and its ability to forage in the benthic zone is limited. In fact, Hudjetz *et al.* (2008), in laboratory experiments, found that populations of *Daphnia magna*, despite being able to survive only by the consumption of periphyton, showed a strong food preference for phytoplankton and only resorted to the consumption of periphyton when the phytoplankton concentration dropped to values below 0.05 mg/L. In addition, Hudjetz *et al.* (2008) observed that, in experiments with the two food sources, phytoplankton and periphyton, zooplankton biomass was greater when compared to similar experiments with only phytoplankton as a food source. The authors argue that predation of *Daphnia magna* on the periphyton can stabilize its population density and provide competitive advantages over other organisms of the order Cladocera.

It is evident that the proposed model ignores many phenomena that can interfere with the observed patterns, such as the presence of inedible algae (Kretzschmar *et al.* 1993) and the presence of zooplankton predators (Scheffer 1991). It would be interesting to expand the model proposed in this work, including those effects and also modeling the differences between the nutritional quality of phytoplankton and periphyton to zooplankton. Despite the limitations of the model, our results emphasize the role of habitat coupling and contribute to the understanding of processes and mechanisms capable of promoting stability to population dynamics in shallow lakes. If multi-chain omnivory does have stabilizing effects on population dynamics across diverse habitats, then drastic population reduction or extinction in any compartment can have profound ecosystem effects in large-scale contexts.

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## SUPPLEMENTARY MATERIAL

**Table S1.** Definition of the model parameters with their respective values, which were obtained from Scheffer (1991) and Rose *et al.* (1988).

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