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The role of habitat coupling on the stability of population

dynamics in shallow lakes

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Summary

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 analyze 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 use a Lotka—Volterra type model of zooplankton and algae, explicitly modeled as phytoplankton and periphyton. Zooplankton can eat on 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) natural zooplankton—algae systems tend to be stable up to high nutrient values at certain degrees of omnivory, that (2) algae exchange among compartments may dampen stability and that (3) exploitative 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 the understanding of processes and mechanisms capable of promoting the stability of population dynamics in shallow lakes.

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

Resumo

Os mecanismos responsáveis pela estabilidade populacional de pequenos lagos rasos, sem peixes e com alta produtividade de algas ainda não foram propriamente entendidos. Estudos publicanos nesse tema negligenciam o papel do acoplamento entre os habitas pelágico e bentônico, um fenômeno que possui efeitos notáveis na estabilidade populacional de ecossistemas aquáticos. Por isso, criamos um modelo simples para mostrar que o acoplamento entre os habitas bentônico e pelágico pode explicar discrepâncias entre resultados de modelos predador-presa clássicos e padrões observados em sistemas aquáticos naturais. Usamos um modelo do tipo Lotka-Volterra de zooplâncton e algas, explicitamente modeladas como fitoplâncton e perifíton. O zooplâncton pode se alimentar de algas presentes em ambos compartimentos, bentônico e pelágico, apresentando uma configuração onívora de cadeias múltiplas, enquanto o fitoplâncton e o perifíton se envolvem em competição exploratória à medida que a capacidade de suporte do sistema aumenta. Também modelamos a troca de algas entre os compartimentos. Os resultados do nosso modelo mostram que (1) sistemas naturais de alga—zooplâncton tendem a ser estáveis até altos valores de capacidade de suporte em certos graus de onivoria, que (2) a troca de algas entre os compartimentos pode diminuir a estabilidade e que (3) a competição exploratória entre o fitoplâncton e o perifíton também pode diminuir a estabilidade. Os resultados do modelo são suportados por resultados empíricos disponíveis na literatura. Apesar das limitações intrínsecas da modelagem de sistemas naturais, nossos resultados enfatizam o papel do acoplamento de habitat e contribuem para o entendimento de processos e mecanismos capazes de promover a estabilidade da dinâmica populacional em lagos rasos.

Palavras-chave: Omnivoria, Zooplâncton, Fitoplâncton, Perifíton, Modelagem matemática.

Introduction

Population stability is an important metric for the study of population dynamics. It can inform about populations in danger of local extinction and it is closely related to the decline in the Earth's biodiversity (Mccann 2000). This metric 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 proves to be extremely complex. Several elucidations have been proposed for this concept, the most applied being those that involve the relative variability of a population as a function of space and/or time. 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, it is a key part in the distinction between the natural stochastic variations and the ecosystem responses to anthropic environmental changes (Yang et al. 2019).

One of the first well-defined concepts in the study of populations in ecology was the development of dense-dependent models that relate the size of a population to the carrying capacity of the environment (Lotka 1910). Another important advance was the perception that dense regulatory mechanisms could generate population cycles or even aperiodic fluctuations (May 1974). Since then, some studies, such as Hassell et al.(1976) and Mueller & Ayala (1981), suggested that most natural populations appeared to have a stable equilibrium that tended to a limited value depending on the carrying capacity of the environment. However, other subsequent works (Turchin & Taylor 1992, Bjornstad et al. 1996) have suggested that unstable population dynamics could be more common than earlier studies had supposed. Currently, there are

numerous examples of stable and unstable populations in nature (Mccann 2000). Several mechanisms capable of stabilizing or destabilizing populations are known. One of these mechanisms that has been gaining increasing importance in the study of populations and communities in recent decades is called omnivory (Pimm 1978, Vanni et al. 2005). Having several definitions, omnivory can be described as the adaptive foraging of a consumer, that is, to be able to switch between different sources of food based on difficulty, relative availability, and preference (Vadeboncoeur et al. 2005). However, the most commonly accepted definition is that omnivores feed on more than one trophic level within the same food chain (Pimm 1978). Nevertheless, 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 and Scheuerell 2002, Liu et al. 2020).

There is a debate among researchers 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. This prey, therefore, will be at greater risk of local extinction due to the fact that its in a habitat with a high density of its predator (Pimm 1978, Vanni et al. 2005). However, the idea that population stability is directly proportional to the amount of energy pathways or connections in the trophic webs that characterize any community is an axiom accepted by many ecologists (MacArthur 1955, Paine 1969, May 1974). 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 Lokta-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. Despite the mentioned models predict 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 as key for stabilizing algae-zooplankton population dynamics in aquatic ecosystems, such as: the presence of large amounts of inedible algae in eutrophic lakes (Kretzschmar et al. 1993), the fact that the zooplankton biomass is not uniformly distributed in the lake volume, but concentrated in mobile spots (De Boer & Scheffer 1995) and the top-down effect of zooplanktivorous fish, in which top predators prevent zooplankton biomass from increasing to the point of locally extinguishing phytoplankton. This top-down effect is one of the most studied factors as responsible for enhancing population stability in lakes with high algae productivity (Scheffer 1991, Schindler & Scheuerell, 2002, Vander Zanden & Vadeboncoeur 2002, Vadeboncoeur et al. 2005, Vanni et al. 2005), in which top predators prevent zooplankton biomass from increasing to the point of locally extinguishing phytoplankton. Yet, stable balances of these populations are observed in nature even in high-productivity lakes, without zooplankton predators and the without 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, its 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 theme 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 in shallow lakes (Schindler & Scheuerell 2002, Vander Zanden & Vadeboncoeur 2002, Vasconcelos et al. 2016, 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 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 (Wetzel 1983). Periphytic algal communities are more developed in clear and shallow water bodies as sunlight is able to reach the benthic region. This implies in a competitive relation for light between planktonic 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 periphyton algae caused by wind are forms of habitat

coupling that may have noticeable consequences for population dynamics (Tunney et al. 2018).

In this study, 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 a 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 zooplanktonic multi-chain omnivory. Our goal is to evaluate how the benthic-pelagic coupling will affect the population dynamics, particularly, its effect on population stability.

Methods

Model formulation

Scheffer (1991), based on the works of Holling (1959), Lotka (1910) e Rose et al. (1988), proposed a system of first-order ordinary differential equations to simulate algae-zooplankton population dynamics, such as:

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

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

In which:

PP = Algae biomass (mg/L)

r = Maximum growth rate of phytoplankton (day^{-1})

Kt = Carrying capacity (mg/L)

g_z = Maximum grazing rate of zooplankton on algae (day^{-1})

h_{PP} = Monod's saturation constant (mg/L)

Z = Zooplankton biomass (mg/L)

e_z = Prey assimilation efficiency of zooplankton

m_z = Rate of zooplankton mortality and respiration (day^{-1})

Equation (1) refers to phytoplankton (PP). The first term of the equation is based on the Lotka-Volterra logistic growth. In the absence of zooplankton, the concentration of algae would reach a maximum value limited by the carrying capacity of the lake: PPmax = (rPP · (1-PP / K)). The second term of equation (1) is a Monod function, specific for the growth of microorganisms, which represents the consumption of algae by zooplankton. The intensity of this predation is dependent on the phytoplankton concentration, which characterizes a type II functional response (Holling 1959).

Equation (2) refers to zooplankton (Z). The first term of this equation is the same as the second term of equation (1) but multiplied by the efficiency of conversion of

ingested biomass into growth (e_z). That is, the entire predated phytoplankton biomass is transformed, with a certain conversion efficiency, into zooplankton biomass. The second term of equation (2) represents the death of zooplankton by cell aging. Scheffer (1991) also incorporated fish predation in zooplankton into his model, however, since the objective of this study is to simulate food webs without zooplankton predators, these terms were removed from the model.

To add the multiple-chain omnivory to the simulation, it was necessary to break equation (1) into two, one for the phytoplankton and the other for the periphyton. 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 be included in the model was the shading of the benthic region caused by phytoplankton. As the concentration of pelagic algae increases, the water column becomes more turbid, and less light reaches the benthic region, thus reducing photosynthesis in that region, which consequently limits the periphyton growth. A representative diagram of the food web to be studied is shown below in figure 1.
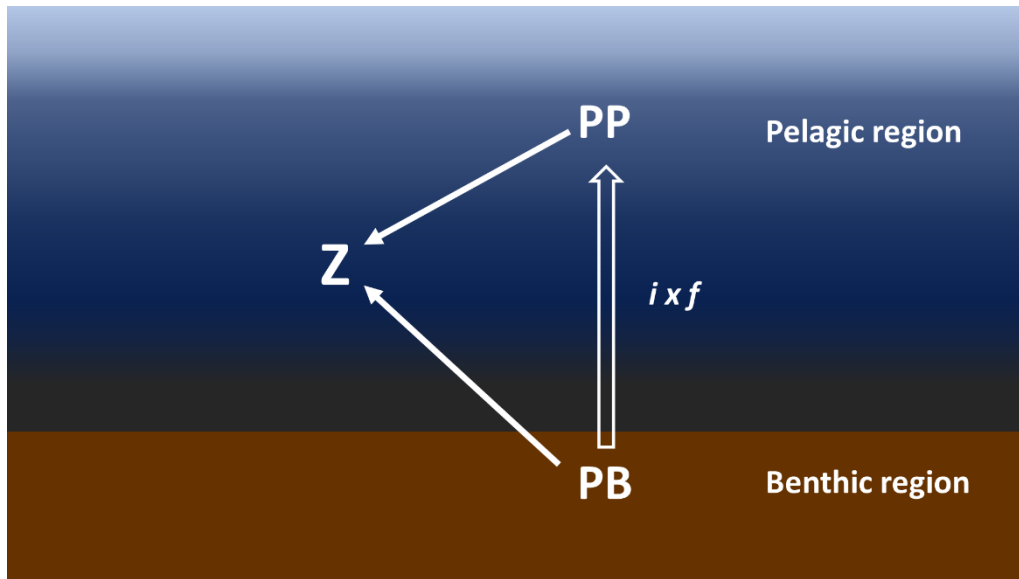
Fig. 1: Spatial configuration of the model. Zooplankton (Z) is able to feed on both phytoplankton (PP) and periphyton (PB). Despite the prey being confined in their environments, there is a contribution of biomass, due to the movement of the water column, from the periphyton to the phytoplankton, represented 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.

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 δ_{PB}, multiply the terms referring to zooplankton feeding. However, δ_{PP} was included only in the terms referring to the herbivory in the pelagic zone and δ_{PB} only in the terms referring to the herbivory in the benthic zone. 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 of one food source in relation to the other. The parameterization of these factors was based on:

a) As the concentration of one food source increases in relation to the other, the likelihood of consumption of that food source (phytoplankton or periphyton) also increases.

b) A variable referring to the intensity of the zooplankton omnivory (π) was included. For $\pi = 1.00$ and $\pi = 0.00$ there are no omnivory and the zooplankton only feed in the pelagic or benthic zone, respectively. For intermediate values of π, both preys are consumed. For $\pi = 0.5$, omnivory is maximum and the zooplankton's food preference is given only by the relative availability of the food sources. By varying π from 0.50 to 1.00, we can regulate the strength of omnivory and test more comprehensively how this behavior interferes with the population dynamics of both resources

The equations for the δ_{PP} e δ_{PB} factors are below:

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

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

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):

$$bp = 1 - mxp \tag{5}$$

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

Where:

bp = Minimum proportion of the carrying capacity attributed to benthic production

mxp = Maximum proportion of the carrying capacity attributed to pelagic production

K = carrying capacity (mg/L)

θ = 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:

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

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

$$\frac{dZ}{dt} = \delta_{PP} \cdot e_z \cdot g_{zPP} \cdot Z\frac{PP}{PP + h_{PP}} + \delta_{PB} \cdot e_z \cdot g_{zPB}$$

$$\cdot Z\frac{PB}{PB + h_{PB}} + \delta_{PP} \cdot e_z \cdot g_{zPB} \cdot Z\frac{ifPB}{ifPB + h_{PB}} - m_z Z \tag{9}$$

The terms PP and PB refer to the phytoplankton and the periphyton, respectively. The table below describes all the variables in the model with their respective assigned values. These values were obtained from Scheffer (1991) and Rose et al. (1988).

Table 1 - Definition of the model parameters with their respective values.

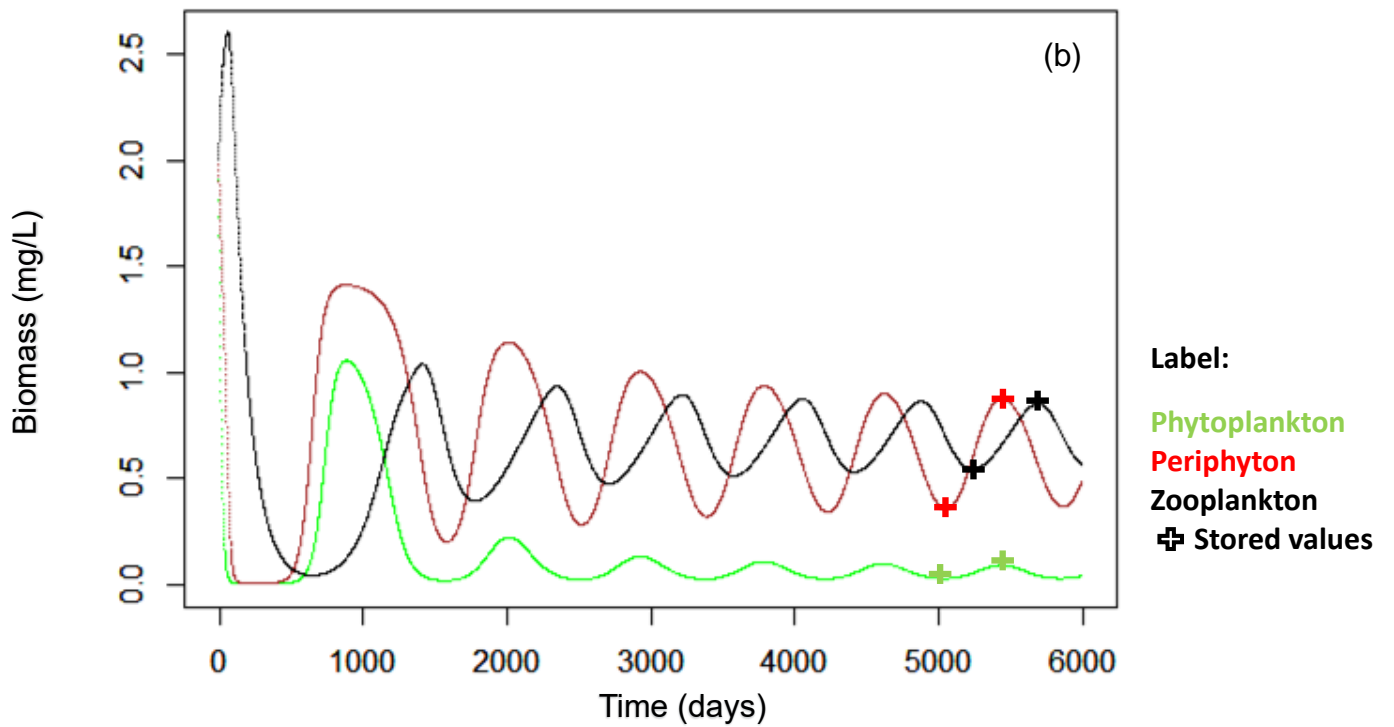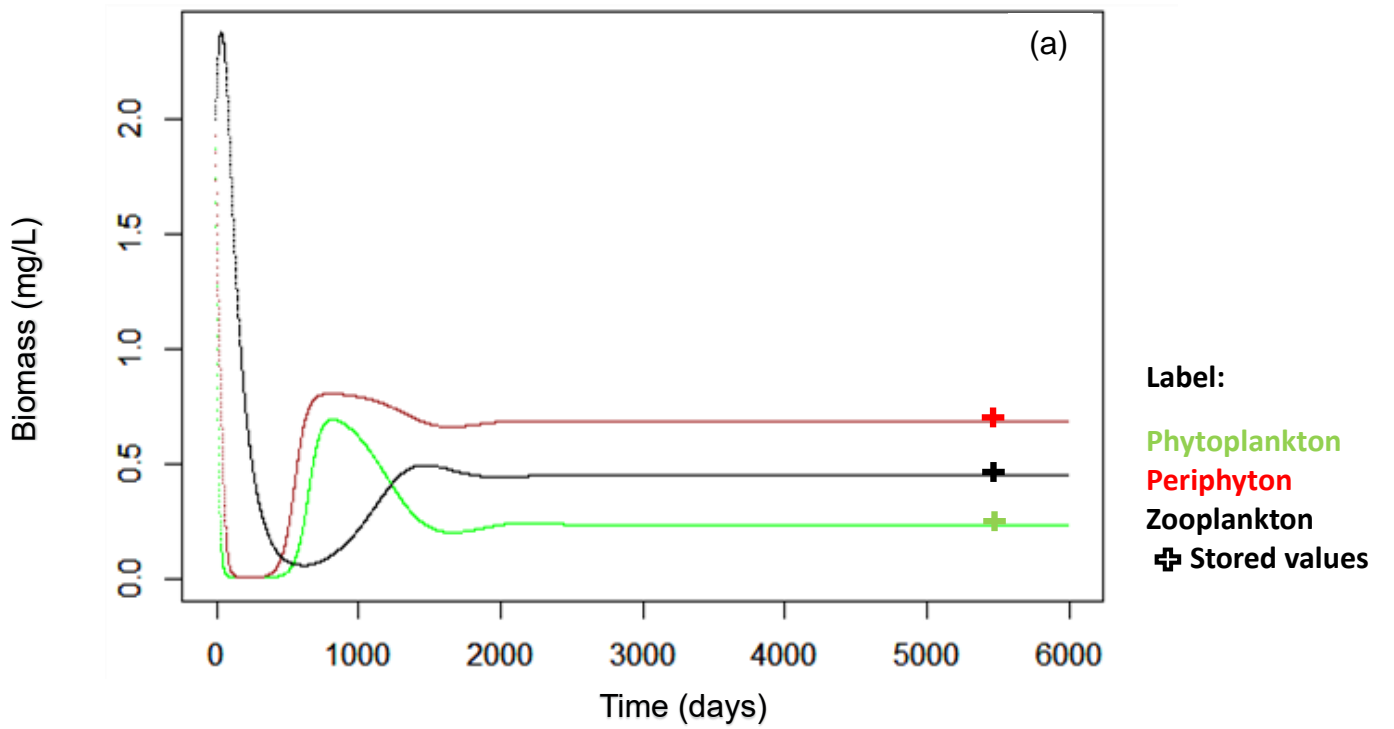| Symbol	definition	Value(s)
r_j	Maximum growth rate of phytoplankton	0.5/day
K	Carrying capacity	0 – 5 mg/L
δ	Prey preference	Described in the text, equations (3) and (4)
g_{zj}	Maximum grazing rate of zooplankton on algae	0.8/day
h_j	Monod's saturation constant	0.6 mg/L
i	Mixing rate of the water mass	0.25/day 0.50/day 0.75/day 1.00/day
f	Proportion of benthic algal forms susceptible to removal by the water movement	0.1
e	Prey assimilation efficiency of zooplankton	0.6
m_z	Rate of zooplankton mortality and respiration	0.175/day
p	Proportion of the carrying capacity attributed to the phytoplankton	Described in the text, equation (6)

mxp	Maximum proportion of the carrying capacity attributed to pelagic production	Low competition: 0.60 High competition: 0.80
Bp	Minimum proportion of the carrying capacity attributed to benthic production	Low competition: 0.40 High competition: 0.20
θ	scattering angle coefficient of the incident light beam in the water	2
π	Intensity of omnivory	0.50 0.75 0.90 1.00

Numerical analysis

The simulations were carried out with the aim of analyzing the relationship between habitat coupling and population stability in a simple three-species bi-trophic food web. The processes that represent the coupling between the benthic and pelagic habitats in the model and their respective parameters are the intensity of omnivory (π), the rate of mixing of water mass (*i*), and the intensity of competition for light (mxp).

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.

At first, the system of differential equations was run as a function of time (figure 2), simulating about 6000 days of trophic relations between the three organisms. After the first 5000 days of simulation, it was graphically visible that the populations of zooplankton and primary producers (pelagic: phytoplankton; benthic: periphyton) had reached a steady or periodic oscillatory state. When the simulation was over, the maximum and minimum values of the concentrations between the 5000th and the 6000th day were stored for each organism. Then, the system of differential equations was run again to an infinitesimally higher value of carrying capacity (K) and the minimum and maximum values of the biomass concentrations of the studied organisms were stored once again. This process was done starting with the value 0.00 mg/L of carrying capacity (K) and increasing it by infinitesimal increments up to 5 mg/L. For each increment in the value of K, we stored the maximum and minimum values of the biomass concentrations of the studied organisms after each simulation has reached the final state of behavior (between the 5000th and 6000th day).

(a)

Biomass (mg/L)

Time (days)

Label:

Phytoplankton
Periphyton
Zooplankton
✚ **Stored values**

(b)

Biomass (mg/L)

Time (days)

Label:

Phytoplankton
Periphyton
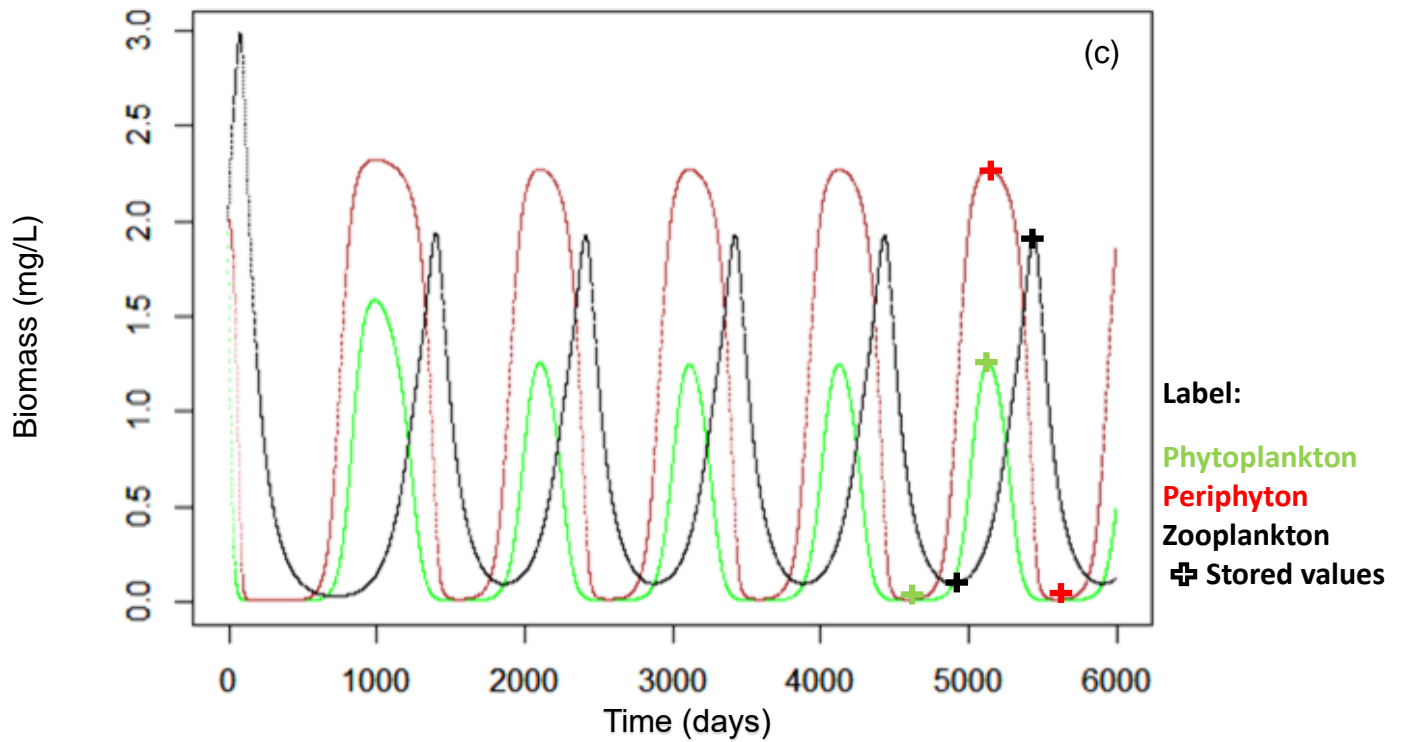**Zooplankton**
✚ **Stored values**

Fig. 2: Zooplankton, phytoplankton, and periphyton biomass concentrations as a function of time simulated for conditions with low (a), medium (b), and high (c) carrying capacity.

   With these different values of maximum and minimum obtained over the range

of variation of the carrying capacity (K), bifurcation diagrams were generated (Figure

3). These diagrams graphically represent all the maximum and minimum values over

the range of variation of the studied parameter. In this way, it is possible to easily

visualize the population stability. If the maximum and minimum values are close to or

even the same, this represents a population with little or no oscillatory behavior. This

stability is observed in the bifurcation diagrams in the interval in which the x-axis has

only one y-axis value (maximum and minimum points are the same). However, in the

interval in which the x-axis has more than one y-axis value, there is, then, oscillatory

behavior (maximum and minimum points are different). The more distant these values

are, the greater the amplitude of the oscillation. The x-axis value at which the system

changes from a stable to oscillatory behavior is called the hopf bifurcation point,

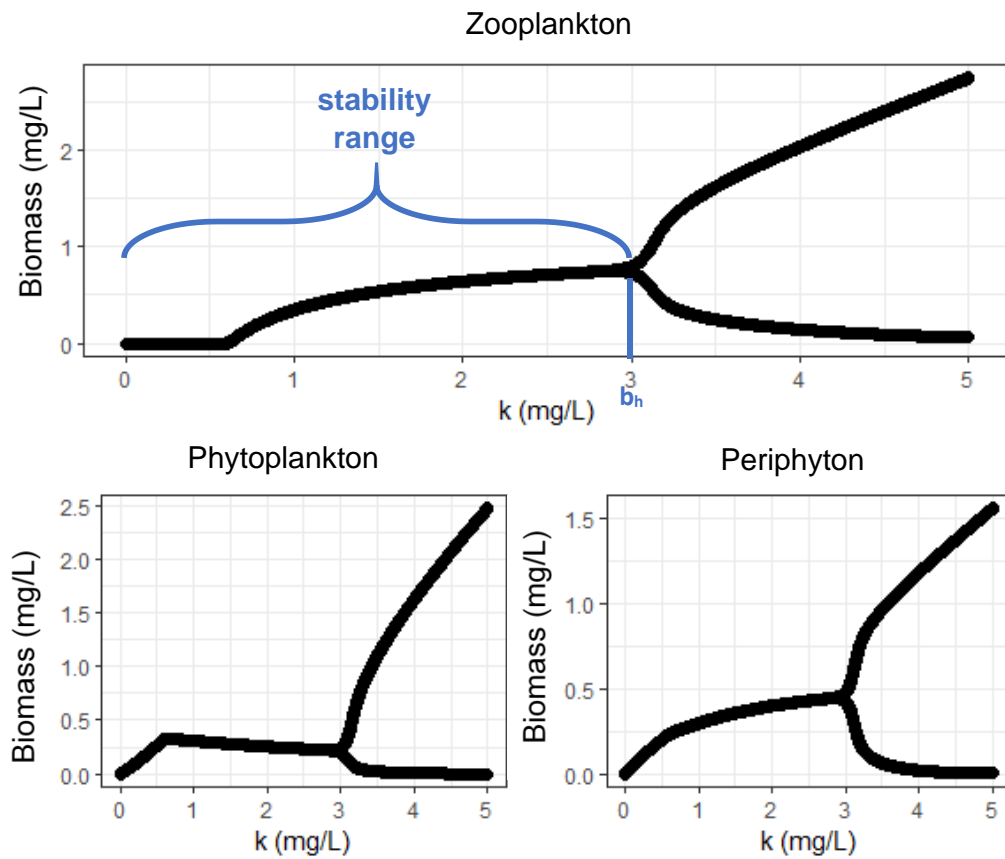identified below in this work as b_h.

Fig. 3: Bifurcation diagrams of the maximum and minimum values of biomass obtained over an interval of carrying capacity. It is noticed that the populations present stability up to approximately 3.0 mg/L (hopf bifurcation point) of carrying capacity, after that, the oscillations begin and the system switches to unstable behavior.

To study how the variation of parameters: intensity of omnivory (π), mixing rate of water mass (i), and intensity of competition for light (mxp) alter population stability, bifurcation diagrams were generated for four values of π, four values of i and two values of mxp, totaling 32 diagrams (figures 4 and 5). The values of π were chosen to enable a maximum omnivory condition ($\pi = 0.50$) and gradually approach the null omnivory ($\pi = 1.00$) in which the zooplankton feeds only in the pelagic zone. Values less than $\pi = 0.50$ were not considered because this would imply conditions in which zooplankton would prefer to feed largely in the benthic zone, and there is no evidence in the literature to demonstrate such a theoretical possibility(Hudjetz et al. 2008, De Kluijver et al. 2015). On the contrary, the evidence supports that, although zooplankton has the ability to feed in the benthic region, it feeds mostly in the pelagic region, appealing to benthic algae only when the phytoplankton concentration is low (Schindler & Scheuerell 2002, Vadeboncoeur et al. 2005, Hudjetz et al. 2008).

For the mixing rate of water mass, we chose values that include conditions of low movement to the high movement of the water column. Regarding the competition for light, we chose to simulate two conditions: one in which the maximum proportion of the total carrying capacity of the lake (K) attributed to the pelagic zone reaches up to 60%, simulating relatively more shallow and transparent lakes. And another in which this proportion reaches up to 80%, simulating relatively less shallow and transparent lakes. As this work is focused on the coupling between pelagic and benthic habitats through the periphyton algae in shallow lakes, we chose not to simulate extreme conditions of competition for light, in which almost no sunlight reaches the benthic region. The stipulated values of the intensity of omnivory (π), mixing rate of water mass (i) and intensity of competition for light (mxp) are shown in table 1.

In order to quantify and compare the population stability, the bifurcation

diagrams were generated as a function 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 their

elevated concentrations 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 diagrams.

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

(x-axis value of the hopf bifurcation point). The higher the carrying capacity at which

the oscillations begin (b_h), the more robust the system stability is.

Results

All the bifurcation diagrams generated by the simulations are consistent with classic

results from other modeling studies of population dynamics in shallow lakes (Scheffer

1991, Vadeboncoeur et al. 2005), in which the algal density grows as a function of the

carrying capacity (in which there is 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 risk of local.

It was observed that the carrying capacity values of the hopf bifurcation points

decreased as the mixing rate of water mass increased (figures 4 and 5), indicating a

possible destabilizing effect of the mixing rate of water mass on population dynamics.

Note that the highest values for b_h were obtained for $i = 0.25$ and the lowest values for $i = 1.00$ (figures 4 and 5).
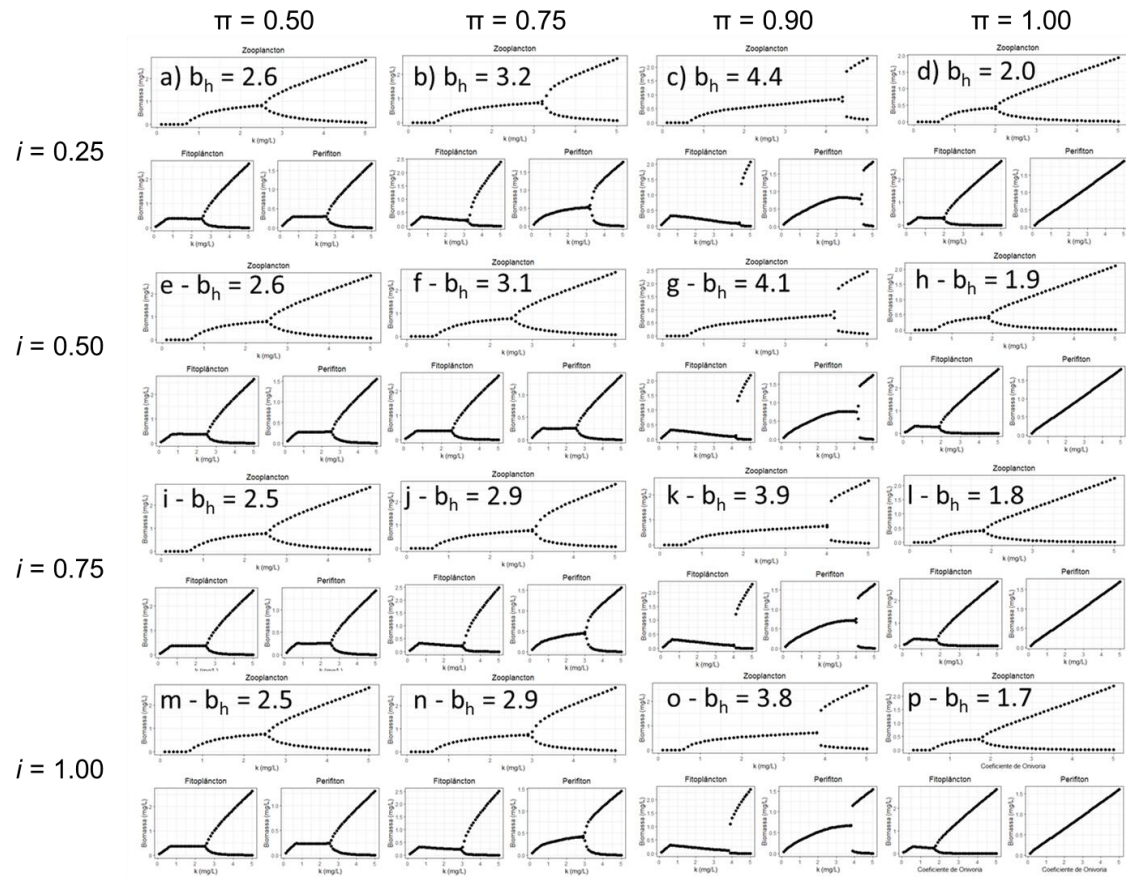
Fig 04: Bifurcation diagrams generated for a condition of low competition for light. The values of intensity of omnivory (π) increase from left to right and the values of mixing rate of water mass (i) increase from bottom to top. At the top-left of each graph, there is an identification letter and the value of the hopf bifurcation point (b_h).
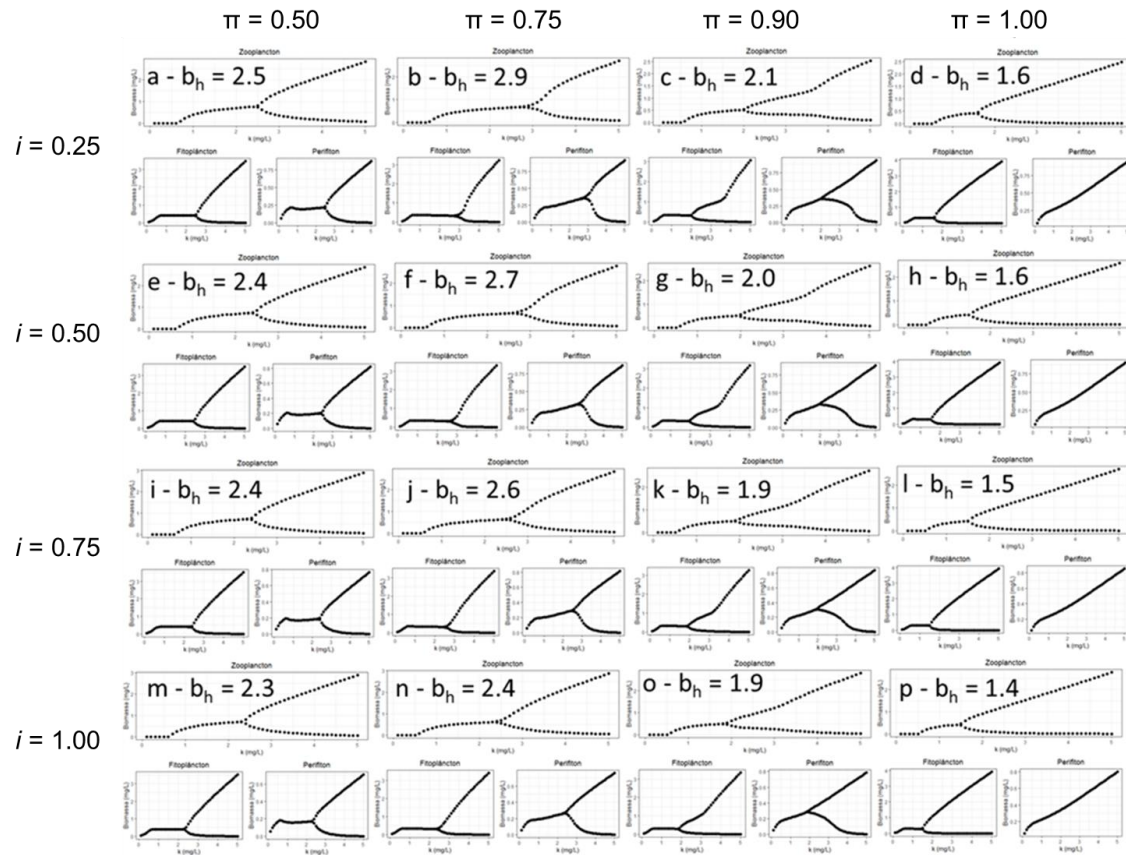
Fig 05: Bifurcation diagrams generated for a condition of high competition for light. The values of intensity of omnivory (π) increase from left to right and the values of mixing rate of water mass (i) increase from bottom to top. At the top-left of each graph, there is an identification letter and the value of the hopf bifurcation point (b_h).

Intermediate intensity values of multi-chain omnivory (π), in the analyzed interval $\pi = [0.50; 1.00]$, were the ones that presented the highest values of b_h. For the condition of low competition for light (figure 4), the highest values of b_h were obtained at $\pi = 0.90$ and for the condition of high competition for light (figure 5), at $\pi = 0.75$, suggesting that greater intensity of omnivory is needed to maintain stability as less light reaches the benthic region. 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 (figures 4 and 5). Comparing the bifurcation diagrams c and d of figure 4, for example, we can see a big difference in the values of b_h, being 4.4 and 2.0 mg/L respectively. In other words, keeping all other parameters constant between the two diagrams and varying only the intensity of multi-chain omnivory, the system's stability interval increased by 120%. The diagram d in figure 4 is the result of a simulation in which there is no omnivorous behavior and the zooplankton only feeds on phytoplankton ($\pi = 1.0$), whereas in the simulation of diagram c of the same figure, the intensity of omnivory is such that zooplankton diet consists of 90% phytoplankton and 10% periphyton (if the relative availability of the two food sources is the same).

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 (figure 4) and Mb = 2.20 mg/L and IQR = 0.7 mg/L for the scenario with high competition for light (figure 5), which represents a 25% increase in the median value. Furthermore, if we compare all the b_h values of the diagrams with the same identification letters (figures 4 and 5) between the conditions of low and high competition for light, we will see that the stability range is always greater for the

condition of low competition for light. This suggests that the solar radiation that reaches the benthic region enhances population stability.

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 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).

The axiom that population stability is directly proportional to the number of connections in the trophic webs (MacArthur 1955, Paine 1969, May 1974) 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 of only two trophic levels and three organisms. Such 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, δ_{PP} e δ_{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 (Rose et al. 1988, Rosenzweig 1971, Scheffer 1991). However, the conditions of high intensity of omnivory ($\pi \approx 0.50$) are those that maximize the consumption of algae and, despite the prey preference variables mitigating the population decline of the scarcest food source, the growth of zooplankton may be high enough, that this mitigation is not sufficient to prevent the excessive algae consumption and the subsequent increase in oscillations. 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 (Rosenzweig 1971). 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).

It is interesting to notice that there was an increase in the intensity of the optimal omnivory (the value of π 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 sate with greater benthic communities (Scheffer et al. 2003, Roozen et al. 2007)_. This suggests that the larger the periphyton 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.

We speculate that, despite the existence of a well-developed periphyton algal community in a given lake, the paradox of 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, as

suggested by our results. 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 Cladorera.

It is evident that the proposed model ignores many phenomena that can interfere with the observed patterns. For example, Kretzschmar et al. (1993) showed that the presence of inedible algae under conditions of high algal productivity could contribute to the population stability of zooplankton. However, this study was done in the context of only one food chain and apparently, this effect only occurs in lakes with high levels of eutrophication, in which inedible algae are abundant. De Boer & Scheffer (1995) enhance stabilization in their model by incorporated the fact that the zooplankton biomass is not uniformly distributed in the lake volume, but it is actually concentrated in mobile spots. The increase in water turbidity caused by resuspension is a relevant aspect that intensifies the competition for light (Scheffer et al. 2003, Roozen et al. 2007). Another important mechanism that can decrease oscillations in zooplanktonic populations is fish predation (Scheffer 1991, Vadeboncoeur et al. 2005). Yet, many lakes in tropical coastal regions, especially small fishless lakes with intense maritime influence, may exhibit high algal productivity, but still 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 that can serve as food for zooplankton. In addition, the reduced depth approximates the pelagic and benthic habitats. It would be interesting to expand the model proposed in this work, including effects such as the presence of inedible algae, modeling the differences between the nutritional quality of phytoplankton and periphyton to zooplankton, and incorporating the spatial heterogeneity, previously described as moving spots of zooplankton in the volume of the lake, for example.

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 on population dynamics in shallow lakes. The coupling of habitats has been a phenomenon traditionally ignored in studies of food webs in aquatic ecosystems (Schindler & Scheuerell 2002), nonetheless, its implications have been gaining increasing importance recently (De Kluijver et al. 2015, Devlin et al. 2015, Wang et al. 2019, Liu et al. 2020). 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. Therefore, the monitoring and conservation of lake compartments are gaining increasing importance, and it challenges ecologists to break spacial and multidisciplinary barriers (Vadeboncoeur et al. 2005). The understanding of ecological processes involving zooplankton is particularly important in the current context. In addition to the natural variations in the amount of nutrients in water bodies, an artificial rise in concentrations of dissolved organic matter in aquatic environments around the world has been observed due to the inflow of allochthonous carbon as a result of agricultural and population growth, resulting in an increase in the number of eutrophic lakes with reduced water quality and biodiversity (Monteith et al. 2007). Our results, as

well as those of other authors (e.g. Hudjetz et al. 2008, De Kluijver et al. 2015, Wang et al. 2019), suggest that the food subsidy that periphyton provides for zooplankton can increase the biomass and prevent the local extinction of this herbivore, which in turn plays an important role lake functioning through phytoplankton consumption (Hobbs et al. 2014).

Cited literature

Alboukadel Kassambara, 2020. ggpubr: 'ggplot2' based publication ready plots. R package version 0.3.0. https://CRAN.R-project.org/package=ggpubr

Bjornstad, O., Champely, S., Stenseth, N.C., Saitoh, T., 1996. Cyclicity and stability of Grey-Sided Voles, *Clethrionomys rufocanus*, of Hokkaido: Spectral and principal components analyses. R. Soc. Lond. Philos. Trans. Ser. B 351. https://doi.org/10.1098/rstb.1996.0081

De Boer, R., Scheffer, M., 1995. Implications of spatial heterogeneity for the Paradox of Enrichment. Ecology 76. https://doi.org/10.2307/1941701

De Kluijver, A., Ning, J., Liu, Z., Jeppesen, E., Gulati, R., Middelburg, J., 2015. Macrophytes and periphyton carbon subsidies to bacterioplankton and zooplankton in a shallow eutrophic lake in tropical China: Shallow lake macrophytes-periphyton carbon subsidy. Limnol. Oceanogr. 60, 375–385. https://doi.org/10.1002/lno.10040

Devlin, S., Vander Zanden, J., Vadeboncoeur, Y., 2015. Littoral-benthic primary production estimates: Sensitivity to simplifications with respect to periphyton productivity and basin morphometry. Limnol. Oceanogr. Methods 14. https://doi.org/10.1002/lom3.10080

Grimm, V., Wissel, C., 1996. Babel, or The Ecological Stability Discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323–334. https://doi.org/10.1007/s004420050090

Hassell, M.P., Lawton, J.H., May, R.M., 1976. Patterns of dynamical behaviour in single-species populations. J. Anim. Ecol. 45, 471–486. https://doi.org/10.2307/3886

Hobbs, W., Theissen, K., Hagen, S., Bruchu, C., Czeck, B., Ramstack Hobbs, J., Zimmer, K., 2014. Persistence of clear-water, shallow-lake ecosystems: The role of protected areas and stable aquatic food webs. J. Paleolimnol. 51. https://doi.org/10.1007/s10933-013-9763-1

Holling, C.S., 1959. Some Characteristics of simple types of predation and parasitism. Can. Entomol. 91, 385–398. https://doi.org/10.4039/Ent91385-7

Hudjetz, S., Hammers-Wirtz, M., Strauss, T., Ratte, H.-T., 2008. Periphyton as alternative food source for the filter-feeding cladoceran *Daphnia magna*. Freshw. Biol. 54, 15–23. https://doi.org/10.1111/j.1365-2427.2008.02087.x

H. Wickham. 2016. ggplot2: elegant graphics for data analysis. Springer-Verlag New York.

Jones, J.I., Waldron, S., 2003. Combined stable isotope and gut contents analysis of food webs in plant-dominated, shallow lakes. Freshw. Biol. 48, 1396–1407. https://doi.org/10.1046/j.1365-2427.2003.01095.x

Karline Soetaert, Thomas Petzoldt, R. Woodrow Setzer. 2010. Solving differential equations in R: package deSolve. Journal of Statistical Software, 33(9), 1--25. URL http://www.jstatsoft.org/v33/i09/ DOI 10.18637/jss.v033.i09.

Kretzschmar, M., Nisbet, R.M., Mccauley, E., 1993. A predator-prey model for zooplankton grazing on competing algal populations. Theor. Popul. Biol. 44, 32–66. https://doi.org/10.1006/tpbi.1993.1017

Lancelotti, J., Pozzi, L., Yorio, P., Dieguez, M., Pascual, M., 2009. Fishless shallow lakes of Southern Patagonia as habitat for waterbirds at the onset of trout aquaculture. Aquat. Conserv. Mar. Freshw. Ecosyst. 19, 497–505. https://doi.org/10.1002/aqc.1018

Liu, X., Liu, Y., Wang, H., 2020. Benthic-pelagic coupling in lake energetic food webs. Ecol. Model. 417, 108928. https://doi.org/10.1016/j.ecolmodel.2019.108928

Lotka, A. J., 1910. Contribution to the theory of periodic reaction. J. Phys. Chem. 14 (3): 271 - 274. https://doi.org/10.1021/j150111a004

MacArthur, 1955. MacArthur's 1955 Stability function is related to formal dynamic measures of food web stability. https://doi.org/10.1101/477406

May, R., 1974. Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. Science 186, 645–7. https://doi.org/10.1126/science.186.4164.645

Mccann, K., 2000. The diversity–stability debate. Nature 405, 228–233.

Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., Kopácek, J., Vesely, J., 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450, 537–540. https://doi.org/10.1038/nature06316

Mueller, L., Ayala, F., 1981. Trade-off between r-selection and K-selection in Drosophila populations. Proc. Natl. Acad. Sci. U. S. A. 78, 1303–5. https://doi.org/10.1073/pnas.78.2.1303

Paine, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91–93.

Pimm, S., 1978. Feeding on more than one trophic level. Nature 275, 542–544. https://doi.org/10.1038/275542a0

Polis, G., Strong, D., 1996. Food web complexity and community dynamics. Am. Nat. 147, 813–846. https://doi.org/10.1086/285880

Post, D., Conners, M., Goldberg, D., 2000. Prey preference by a top predator and the stability of linked food chains. Ecology 81, 8-14. https://doi.org/10.2307/177129

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rivera Vasconcelos, F., Diehl, S., Rodríguez, P., Karlsson, J., Byström, P., 2018. Effects of terrestrial organic matter on aquatic primary production as mediated by pelagic–benthic resource fluxes. Ecosystems 21, 1255–1268. https://doi.org/10.1007/s10021-017-0217-x

Rose, K.A., Swartzman, G.L., Kindig, A.C., Taub, F.B., 1988. Stepwise iterative calibration of a multi-species phytoplankton-zooplankton simulation model using laboratory data. Ecol. Model. 42, 1–32. https://doi.org/10.1016/0304-3800(88)90089-0

Rosenzweig, M., 1971. Paradox of Enrichment: destabilization of exploitation ecosystems in ecological time. Science 171, 385–7. https://doi.org/10.1126/science.171.3969.385

Scheffer, M., 1991. Fish and nutrients interplay determines algal biomass: A minimal model. Oikos 62, 271–282. https://doi.org/10.2307/3545491

Scheffer, M., van Nes, E.H., 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia 584, 455–466. https://doi.org/10.1007/s10750-007-0616-7

Schindler, D., Scheuerell, M., 2002. Habitat coupling in lake ecosystems. Oikos 98, 177–189. https://doi.org/10.1034/j.1600-0706.2002.980201.x

Tunney, T., Mccann, K., Jarvis, L., Lester, N., Shuter, B., 2018. Blinded by the light? Nearshore energy pathway coupling and relative predator biomass increase with reduced water transparency across lakes. Oecologia 186. https://doi.org/10.1007/s00442-017-4049-3

Turchin, P., Taylor, A., 1992. Complex dynamics in ecological time series. Ecology 73, 289–305. https://doi.org/10.2307/1938740

Vadeboncoeur, Y., Mccann, K., Vander Zanden, J., Rasmussen, J., 2005. Effects of Multi-chain omnivory on the strength of trophic control in lakes. Ecosystems 8, 1–12. https://doi.org/10.1007/s10021-003-0149-5

Vander Zanden, J., Vadeboncoeur, Y., 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83, 2152–2161. https://doi.org/10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2

Vanni, M., Arend, K., Bremigan, M., Bunnell, D., Garvey, J., González, M., RENWICK, W., Soranno, P.A., STEIN, R., 2005. Linking landscapes and food webs: Effects of omnivorous fish and watersheds on reservoir ecosystems. Bioscience 55. https://doi.org/10.1641/0006-3568(2005)055[0155:LLAFWE]2.0.CO;2

Vasconcelos, F.R., Diehl, S., Rodríguez, P., Hedström, P., Karlsson, J., Byström, P., 2016. Asymmetrical competition between aquatic primary producers in a warmer and browner world. Ecology 97, 2580–2592. https://doi.org/10.1002/ecy.1487

Wang, T., Wang, Q., Xia, S., Yan, C., Pei, G., 2019. Response of benthic algae to environmental conditions in an urban lake recovered from eutrophication, China. J. Oceanol. Limnol. 38. https://doi.org/10.1007/s00343-019-8362-z

Wetzel, R.G., 1983. Recommendations for future research on periphyton, in: Wetzel, R.G. (Ed.), Periphyton of freshwater rcosystems. Springer Netherlands, Dordrecht, pp. 339–346.

Yang, Q., Fowler, M., Jackson, A., Donohue, I., 2019. The predictability of ecological stability in a noisy world. Nat. Ecol. Evol. 3, 1. https://doi.org/10.1038/s41559-018-0794-x