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A trophic chain model with the inclusion of a nutrient, a prey and a predator, applied to the Lake Maracaibo ecosystem

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Abstract

We present a trophic chain model that describes the invasion of *Lemna obscura* (a duckweed) in Lake Maracaibo. We consider a prey (the *Lemna*), with a predator (a herbivore), and we include an explicit equation for a nutrient. It is noteworthy that our model does not present some well-known paradoxes such as Rosenzweig's enrichment paradox, and Luck's unstable low prey paradox. We find that both stable nutrient and *Lemna* equilibrium populations are proportional for small nutrient influx. For higher flux input, the *Lemna* population grows linearly with nutrients, but a stable predator population requires a threshold nutrient density. We suggest that the huge amounts of *Lemna* in Lake Maracaibo could be profitable as an important protein source for manufacture of manure, and also for animal and/or human nutrition.

Key words: human profitability; predator; prey; paradox, protein source; trophic chain.

Un modelo de cadena trófica, con la inclusión de un nutriente, una presa y un depredador aplicado al ecosistema del lago de Maracaibo

Resumen

Se presenta un modelo de cadena trófica que describe la invasión de *Lemna obscura* (una lenteja de agua) en el lago de Maracaibo. Se considera una presa (la *Lemna*) y un depredador (un herbívoro), y se incluye una ecuación explícita para el nutriente. Una característica importante de nuestro modelo es que este no presenta la paradoja de enriquecimiento de Rosenzweig, ni la paradoja de ausencia de población pequeña estable de presa de Luck. Se encuentra que las poblaciones estables de presa y nutriente son proporcionales para concentraciones pequeñas de este. Para concentraciones mayores del nutriente, la población de *Lemna* crece linealmente con el flujo de ingreso de nutrientes; sin embargo, la existencia de una población estable del depredador requiere una densidad umbral del nutriente y, por lo tanto, de presa. Se sugiere que las ingentes cantidades de *Lemna* que existen en el lago de Maracaibo podrían ser aprovechadas como fuente importante de proteínas en la fabricación de abonos y también en nutrición animal y humana.

Palabras clave: Aprovechamiento humano; cadena trófica; depredador; fuente de proteínas; paradoja; presa.

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Introduction

Lemna or duckweed is a plant of the araceaus order, family lemnaceae, with 6 genres and 38 species. This order includes the tiniest existing flowering plants. They can reproduce themselves sexually by polinization, or asexually, by gemation. Many species resemble little green shavings. They live in tropical or subtropical environments and a great number of varieties exist in Venezuela (1). They feed on nitrogen and phosphate wastes taken up from polluted water (2, 3, 4, 5) and they produce big amount of biomass (6, 7, 8). Duckweed is an important source of essential amino acids, and there are detailed studies on its utilization as animal foodstuff (9, 10, and the references therein). Duckweeds are very sensitive to some toxics (11, 12), and they are currently used in bioassays for measuring the pollution level of freshwater reservoirs and the existence in a region of dangerous chemical compounds (13, 14, 15). *Lemna* growth depends also on seasonal daily radiation, and their appearance usually coincides with the sunniest months each year. Uncontrolled duckweed growth may lead to freshwater eutrophization. During the first half of 2004, a *Lemna* patch covered an important portion of the surface of Lake Maracaibo. Duckweed episodes have been repeated in 2005 y 2006. Lake Maracaibo has an approximate area of 13.300 Km^2, and a volume of 280 million cubic meters, a large part of which is heavily degraded. The magnitude of the duckweed invasion suffered by the largest freshwater volume in South America caught our interest, and we developed a model describing duckweed behavior, with the inclusion on nutrients, and a predator feeding from it. We propose a very simple, three level trophic chain, each one described by a coupled differential equation.

There is a good deal of literature on trophic chains, and we limit ourselves to mention only some of them, dealing with stability and bifurcation analysis (16, 17), and with chaotic behavior (18). Stability, asymptotical behavior and extinction scenarios, in particular mutual extinction and a disagreement with the Luck low density paradox, are discussed in (19), (the existence of a well behaved equilibrium point is also proved in that work). Existence of equilibrium points, stability and determination of phase pictures are dealt with in (20), but in that work numerical restrictions are imposed on the parameters ruling the system. A question remains as to the phenomenological justification for the inclusion in those articles of a Michaelis-Menten type response. For a study of exploitation ecosystems based on predator and prey isoclines, see (21) and the references therein. A study of a trophic chain of *n* sequentially interactive elements, each one described by an ordinary differential equation, is performed in (22). In that article, the authors specify some limiting conditions on each equation determining an interaction between each pair of consecutive terms, after that, they can make predictions for their system global stability. An arbitrarily long food chain is described in (23). The authors now impose uniformity hypothesis for the interaction functions that they use. That approach allows them to study their system stability without restricting the predator-prey interaction to any specific functional form. Validation of models using real data associated with them is a less studied subject, reference (19) being an exception to this. A very complex model for Lake Zapotlán (Mexico) was recently presented (24). That paper includes a careful parameter evaluation, but the very complicated system of differential equations prevents the authors from any qualitative (in the mathematical sense) and/or linear analysis of their system. Other researchers (25) assume the existence and stability of a positive equilibrium point (a equilibrium point is termed positive if all its components are positive), after that the desired study is carried out (sensibility to mortality of their hypothetical equilibrium point and adaptative changes of the model trophic levels).

Given a trophic chain model, it is a lengthy and cumbersome process to find its equilibrium points and to discuss the stability of each one**.** The difficulty is linked to solve one at least grade-three algebraic equation. Many researchers avoid dealing with such a subject, but instead impose well-known restrictions to the parametric functions describing the interaction among their systems diverse components, these conditions assuring the stability of the assumed positive equilibrium point, if it exists. A word is necessary on the intrinsic stiffness of such well-behaved systems.

In this paper, we describe the temporal evolution of a trophic chain under conditions associated with various levels of nutrient, commensal, and predator, and their growth and decay rates. We find the dependence of the equilibrium and stability concentrations, on the parameters ruling the mentioned interactions, we summarize our findings in three theorems, and then we suggest some applications for our model. The remainder of the paper is as follows: we define in part 2 the variables and parameters describing our system, in part 3, we study the equilibrium and stability of the system, and we present our theorems, in part 4, we display some graphics illustrating the results of the precedent chapter. In part 5, we discuss our results, and finally, in part 6 we present our conclusions. Additionally, some mathematical details are outlined in the Appendix.

System

We introduce here the differential equations ruling our system. Variable *X* represents the duckweed; variable stands for the nutrient; and variable *Z* represents a herbivore as predator (tilapia, a fish, for instance) capable of controlling *Lemna* growth; finally, time is represented by τ. All variables and parameters in this system always have non-negative values. We separately discuss in the following the differential equation for each variable. *Lemna*, *X*, grows feeding on the nutrient, *Y*, at a rate a_1XY, duckweed growth is limited in a logistic way (Pearl-Verhulst) $-a_2X^2$, and herbivore (top predator), *Z*, feeds on the *Lemna* and this interaction produces an additional decay $-a_3XZ$, where, a_1, a_2, and a_3 are the respective ruling dynamical coefficients. Therefore, the temporal evolution for duckweed is given by:

$$\frac{dX}{d\tau} = a_1XY - a_2X^2 - a_3XZ \qquad [1]$$

Nutrient, *Y*, is poured into the water at a rate b_1; it degrades down after a time b_2^{-1}, and duckweed takes it at a rate b_3XY, with b_3 as the dynamical interaction coefficient. The equation for the nutrient is then:

$$\frac{dY}{d\tau} = b_1 - b_2Y - b_3XY \qquad [2]$$

Herbivore growth rate is proportional to the duckweed uptake e_1XZ, with e_1 as the dynamical associated coefficient. Herbivores die after a time e_2^{-1}. Then *Z* behaves as:

$$\frac{dZ}{d\tau} = e_1XZ - e_2Z \qquad [3]$$

Note that in a real interaction, all the coefficients in our equations are not constant but variables that depend in a complex way on factors such as nutrient concentration, water temperature and salinity, daily solar radiation, presence of oligosinergic factors, etc.

We now introduce the changes:

$$t = b_2\tau; \quad x = \frac{b_3}{b_2}X; \quad z = \frac{a_3}{b_2}Z;$$

$$\alpha_1 = \frac{a_1}{b_2}; \quad \alpha_2 = \frac{b_2}{a_3}; \quad \beta = \frac{b_1}{b_2}; \quad \gamma = \frac{e_1}{b_3}; \quad \omega = \frac{e_2}{b_2}$$

And our system reduces to:

$$\frac{dx}{dt} = \alpha_1xy - \alpha_2x^2 - xz; \quad x \geq 0, \qquad [4]$$

$$\frac{dy}{dt} = \beta - y - xy; \quad y \geq 0 \qquad [5]$$

$$\frac{dz}{dt} = \gamma xz - \omega z; \quad z \geq 0, \qquad [6]$$

Where $\alpha_1 \geq 0$, $\alpha_2 > 0$, $\beta > 0$, $\gamma > 0$, $\omega > 0$ are the parameters ruling the interactions among the diverse elements of the system. We observe that $z = 0 \rightarrow \frac{dz}{dt} = 0$; this fact means that when $z(t)$ takes this value, it remains unchanged unless additionally perturbed, and similar statements can be made for $x(t)(x = 0 \rightarrow \frac{dx}{dt} = 0)$, while $y = 0 \rightarrow \frac{dy}{dt} > 0$, then it is immediate that system [4] to [6] stays in the first octant of the space if it is initially there. Therefore our study is limited to points in this space (points with biological meaning).

Equilibrium points and their stability

1. General. Equilibrium points for our system are found by equating to zero the right hand side of equations [4] to [6]. Asymptotic stability is discussed by linearization and evaluation of the eigenvalues of the associated Jacobi matrix. We use the Routh-Hurwitz criterion for evaluation of the eigenvalues signs, (26) and Central Manifold Theory, (27) when necessary (null eigenvalues). For mathematical details, see the Appendix.

2. Equilibrium points. In the following, we use a super index asterisk for denoting the respective variable equilibrium values. Our system has three equilibrium points, and we call the null equilibrium point P_0, that one having no *Lemna* population. Then,

$$P_0(x_0^*, y_0^*, z_0^*) = (0, \beta, 0) \qquad [7]$$

This point is unstable if $\alpha_1 > 0$. If $\alpha_2 = 0$, or $\beta = 0$, there are no more equilibrium points, but then P_0 is stable (this is shown by similar methods to that used in the Appendix). The following equilibrium point, P_1, is given by:

$$P_1(x_1^+, y_1^*, z_1^*) = (x_1^*, \frac{\alpha_2}{\alpha_1} x_1^*, 0) \qquad [8]$$

$$x_1^* = -\frac{1}{2} + \frac{1}{2}\sqrt{1 + 4\alpha_1\beta / \alpha_2} \text{ and } x_1^* \neq \frac{\omega}{\gamma} \qquad [9]$$

(observe that P_1 reduces to $(\frac{\alpha_1}{\alpha_2}\beta, \beta, 0)$ for $\frac{\alpha_1}{\alpha_2}\beta << 1$). P_1 is stable if $x_1^* < \frac{\omega}{\gamma}$, and unstable if $x_1^* > \frac{\omega}{\gamma}$.

If $x_1^* > \frac{\omega}{\gamma}$, the system has a last equilibrium point, P_G, which we call the general point because it holds the three non-null variables x, y, z, *Lemna*, nutrient, and predator. This point is given by:

$$P_G(x_G^*, y_G^*, z_G^*) = (\frac{\omega}{\gamma}, \frac{\beta}{1 + \omega / \gamma}, \frac{\alpha_1\beta}{1 + \omega / \gamma} - \alpha_2 \frac{\omega}{\gamma}) \qquad [10]$$

P_G is always stable. Now we define:

$$\beta_m \equiv \frac{\alpha_2\omega}{\alpha_1\gamma}(1 + \frac{\omega}{\gamma}), \qquad [11]$$

When $\beta < \beta_m$, z_G (and therefore P_G) does not exist. Then $\beta = \beta_m$ is the condition of appearance for the predator (threshold condition). An equivalent statement of this fact is:

$$\beta < \beta_m \quad \text{implies} \quad 0 < \frac{\gamma}{\omega} < \frac{\alpha_2}{2\alpha_1\beta}\left(1 + \sqrt{1 + \frac{4\alpha_1\beta}{\alpha_2}}\right).$$

As γ is density predator growth rate for unity of prey attacked, and ω^{-1} is predator mean lifetime, then $\frac{\gamma}{\omega}$ is proportional to the predator's density lifetime increase. Therefore, we conclude that if a predator has a reproduction rate too low, it faces extinction.

Note that: I) the equilibrium concentration z_G^* grows linearly with β. II) z_G^* can be null irrespective of large values of nutrient and duckweed. III) a bifurcation occurs at $x_1^* = \frac{\omega}{\gamma}$, because at that value of x the system evolves from two distinct equilibrium points,

P_0, unstable, and P_1 stable, to three equilibrium points, P_0, and P_1, both unstable, and P_G stable.

3. Particular cases. The following statements can be easily verified by linearization and evaluation of the resulting eigenvalues. If $\alpha_1 << 1$, there is only P_0, stable (this condition can be interpreted as a high aggressive predator, as our variable normalization settled the coefficient of the interaction predator-prey fixed as 1). If $\alpha_2 << 1$, there are P_0, unstable, and P_G ,stable. If $\alpha_2 >> 1$ (very large), equation [4] becomes $\frac{dx}{dt} \approx -\alpha_2 x^2$, uncoupled. Then simple integration shows that $x(t) \to 0$ when $t \to \infty$, and likewise occurs for $y(t)$, and $z(t)$, therefore we have now just P_0, stable. If $\beta = 0$, there exists just (0,0,0), stable, as equilibrium point. If $\gamma << 1$ (or if $\omega \to \infty$), the system has two equilibrium points, P_0, unstable, and P_1, stable. When $0 < \frac{\omega}{\gamma} << 1$, numerical work reveals transient oscillations in x before the system evolves toward its respective equilibrium point.

4. Summary of equilibrium and stability. The results above are summarized in the following three theorems:

Theorem 1. The system [4] to [6]: I) has an unstable null equilibrium point (absence of duckweed, x, and herbivore, z unless $\alpha_1 = 0$, II) has a stable, equilibrium point, with no herbivore, if $x_1^* \leq \frac{\omega}{\gamma}$, this point being unstable in any other situation, III) has a general, non null, stable equilibrium point P_G, stable. If $\beta < \beta_m$, P_G does not exist.

Theorem 2. The system [4] to [6]: I) has only one stable equilibrium point given by $P_0 = (0, \beta, 0)$ in the following cases: $\alpha_1 = 0$, or $\alpha_2 \to \infty$, or $\beta = 0$. (In the first two situations we speak of predator (herbivore) extinction for prey (*Lemna*) exhaustion, but if $\beta = 0$, we call the system "unviable"). II) If $\gamma \to 0$, or if $\omega \to \infty$, the system has two equilibrium points, P_0, unstable, and P_1, stable. III) For the remaining cases there exist the points P_0, unstable, and P_1, stable if $\beta < \beta_m$. If $\beta > \beta_m$, P_0 and P_1, are both unstable, but now appears P_G, stable.

Theorem 3. The system [4] to [6] has a bifurcation at $x_1^* = \frac{\omega}{\gamma}$ (change in the P_1 equilibrium point stability, from stable to unstable, and appearance of P_G, stable, as x_1^* grows up to $\frac{\omega}{\gamma}$).

The plots of equilibrium variables as a function of the nutrient influx β are shown in Figure 1. Figure 1-a shows that there is always a stable, and non null equilibrium value for the *Lemna*, x^*, irrespective of the β value, x_1^*, for $0 < \beta < \beta_m$, and x_G^*, for $\beta > \beta_m$. Then at $\beta = \beta_m$, the bifurcation value for nutrient influx, the complexity of the system grows (a new equilibrium value appears, and the stability of one of the former changes). This fact represents a departure from results reported by Gragnani et al (28), who found that complexity first grows, and then decreases. From Figure 1-b, it is clear that a minimal concentration β_m, of the nutrient is required for the existence of a non-null stable herbivore concentration. Note that this concentration grows linearly with nutrient flow. Then Figure 1 stresses that x_G^* and z_G^* grows with β, the nutrient input. Our system does not present the so-called enrichment paradox described by Rosenzweig (29). However, it is necessary to point out that such a paradox perhaps stems from a misinterpretation.

Numerical integrations

We show now some simulations made with **MAPLE** (Waterloo University, Canadá). Figure 2 shows a stable situation with nutrient and lemma present, but with no herbivore ($\beta < \beta_m$). Figure 2-a shows nutrient growth, Figure 2-b, duckweed, and Figure 2-c, the herbivore which evolves toward its null equilibrium point. A phase diagram is

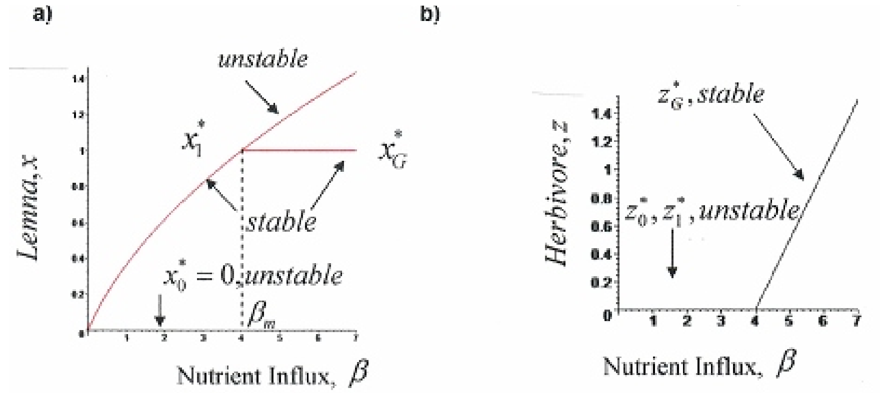

Figure 1. Plots of *Lemna* and herbivore equilibrium concentrations as function of β, the nutrients input into the system. a) There is always a non null, stable equilibrium value x_1^* or x_G^* for the *Lemna*. The null point x_0^* is unstable everywhere. b) A bifurcation occurs at $\beta = \beta_m$, then the complexity of the system grows a step at this point. c) The equilibrium value z_G for the herbivore is always stable, and grows linearly with β. Thus, the paradox of enrichment is not present in our system. Numerical values used in this figure: $\alpha_1 = 1$, $\alpha_2 = \omega = \gamma = 2$, and $0 \leq \beta \leq 7$.

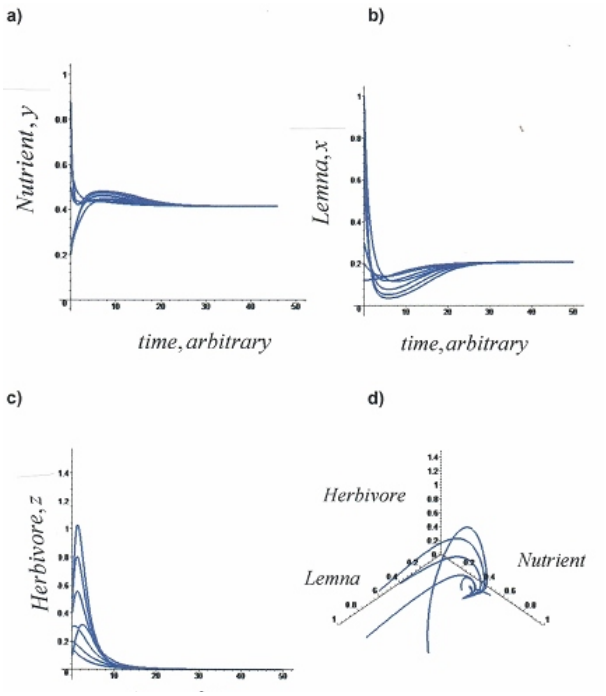

Figura 2. Numerical integrations for P_0 unstable, P_1 stable, and P_G nonexistent ($\beta < \beta_m$). In (2-a) *Lemna* evolves toward its equilibrium stable point; x_1^*; in (2-b) nutrients evolve toward y_1^*. Predator behaves likewise (2-c). Note that x_1^* and y_1^* are both not null, but $z_1^* = 0$, in agreement with equations [8] and [9]. (2-d) shows the system phase picture. This figure exemplifies a situation in which nutrient flux is insufficient to support a predator. Parameter values used: $\alpha_1 = \omega = \beta = 0.5$, $\alpha_2 = 1$, $\gamma = 2$, and a randomly chosen set of diverse initial conditions.

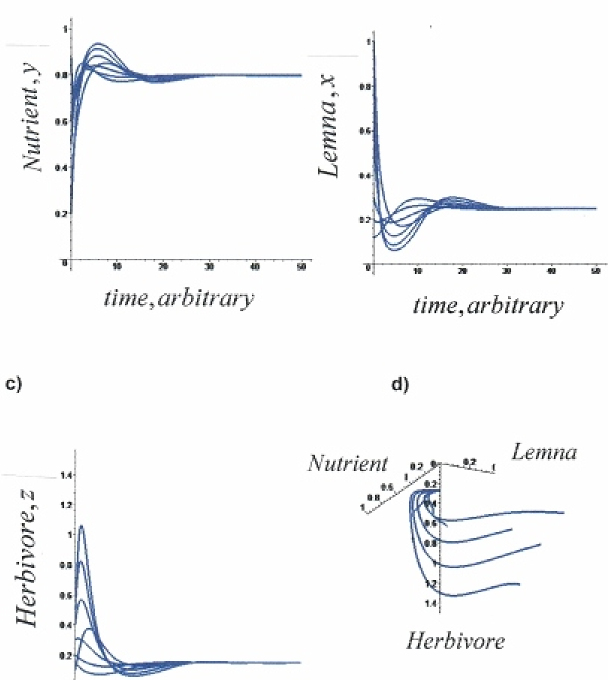

Figura 3. Numerical integrations for P_0 and P_1 both unstable, and P_G stable. Figure (3-a) shows nutrient vs time, Figure (3-b), *Lemna* vs time, Figure (3-c), herbivore vs time, and Figure (3-d) is a phase picture of the system. Irrespective of the initial values, the system evolves toward its equilibrium stable point. Note that (3-a), (3-b), and (3-c) are actually projections of a three-dimensional system on the chosen axis, therefore these curves do not intersect each other when displayed in space. This is easily seen in the three-dimentional phase picture of the system, Figure (3-d). Parameter values for this integration: $\alpha_1 = \omega = 0.5, \alpha_2 = \beta = 1, \gamma = 2$, and a randomly chosen set of diverse initial conditions.

shown in Figure 2-d. In Figure 3 we display a situation with P_0 and P_1 both unstable but P_G stable. Figure 3-a shows the nutrients temporal behavior, Figure 3-b shows the duckweed vs. time, Figure 3-c the herbivore vs. time, and Figure 3-d, the corresponding phase picture. We observe that the system evolves from its initial values towards the only stable equilibrium point. These graphs illustrate the total agreement between mathematical predictions and numerical facts in our model.

Discussion

As the validity of a model depends (among others factors) on its agreement with well-known results and with not presenting unsupported paradoxes, we now check our model with those important facts. We begin discussing mutual extinction, a subject elsewhere treated with a very different model (19). We find mutual extinction when $\alpha_1 << 1$, prey (*Lemna*) rate of reproduction too low (see our equation [9]). Note that our variable normalization settled the coefficient of the interaction predator-prey fixed as 1, then the condition $\alpha_1 << 1$, can also be interpreted as a high aggressive predator, a condition that leads to mutual extinction. There is also extinction when $\alpha_2 \to \infty$ (prey self- inertia too high).There is also extinction when $\alpha_2 \to \infty$ (prey self- inertia too high). We now observe equation [8]. If β is enough small so that a first order series expansion is valid for the square root, then $y_1^* = \beta$, and $x_1^* = \frac{\alpha_1}{\alpha_2}\beta$, that is, nutrient stable equilibrium concentration is determined by its flux input, and *Lemna* stable equilibrium concentration depends on its growth/self-inertia ratio times nutrient flux input (see also Figure 1), but then there is no predator, see Figure (2-c). For higher flux input, however, the situation is more complex (see the equation [9]). *Lemna* equilibrium population, x_G^*, depends only on top predator parameters. Nutrients, y_G^*, grow linearly with $\beta(y_G^* < y_1^*)$, but a stable predator population requires that $\beta > \beta_m$, this means that our system presents a nutrient threshold density for total viability. If our goal was full *Lemna* eradication, this could be achieved by trying $\alpha_2 >> 1$, or $\frac{\omega}{\gamma} << 1$ (Theorem 2), but these possibilities are just mathematical, not biological facts (self-inertia, growth rates, and lifetimes are all non-null and finite). Another possibility is making $\alpha_1 = 0$ (see also Theorem 2). This implies stopping the *Lemna*-environment interaction, or high predation rate. It looks as this possibility has been already repeatedly made (paroxysmal mechanical *Lemna* extraction from the lake), but after each extraction episode *Lemna* returns. Now just the $\beta = 0$ approach remains. *Lemna* could be eradicated stopping the nutrient influx into the lake, and reverting its pollution status, an apparently simple policy. But as simple as this approach seems, we think it is unachievable due to the huge and diverse sources of contamination pouring into the lake (see 18), and also for the implicit task of changing the behavior of communities lacking a conservationalist culture. We see from equation [10] and also from Figure 3, that a system as described in equations [4] to [6] can support a stable, non null equilibrium predator. Such a predator could be a fish (tilapia, for instance) or man, taking the duckweed (regularly) from the lake for later use and profit. Now we deal with paradoxes: Luck biological control paradox states that a system cannot have both a stable and low equilibrium density, but inspection of our equation [10] shows that if both $\beta << 1$, and $\frac{\omega}{\gamma} << 1$, a value of the ratio $\frac{\alpha_2}{\alpha_1}$ can be found so that P_G does exist, and it is stable, therefore our system does not present such paradox. Note also from our equation [10] that predator abundance is proportional to nutrients input, in contradiction with the Rosenzweig paradox (29). This author makes a geometrical analysis of a system predator (P)-prey (V), without an explicit differential equation for the predator, and lacking of a null equilibrium point (no prey, no predator). He then uses a nullcline based approach for discussing six models, all but one, Pearl-Verhulst (logistic) or Gompertzian, and he proves that the unique equilibrium point in his systems becomes unstable when the nutrients flux grows. Such geometrical approach could be right, but we add a different interpretation. Bidimensional models usually have two equilibrium points, the null point, unstable for logistic and Gompertzian models, and a general, not null equilibrium point, which stability depends on the relations among the parameters ruling the system. As the null equilibrium points of the previous cited models remains unstable, the expected conclusion is "*if nutrients influx in logistic or Gompertzian models grows, all grows*". For an additional discussion, rooted in Rosenzweig's method and useful references, see (22). An illustrative discussion on Gompertzian growth can be found in (30).

Conclusions

1) *Lemna* will spread to the whole region where nutrients exist, then it is necessary to avoid nutrient accumulation. The equilibrium point becomes arbitrarily small by making $\beta = 0$, see equation [5]. Alternatively could be made small by finding a way of blockading the *Lemna*-nutrient interaction, see equation [4].

2) It is well known that *Lemna* is very susceptible to certain toxics. Notwithstanding, it does not seem a wise policy to make the pollution in the lake worse by adding an additional harmful substance, which can stay in solution for a unknown period of time.

3) An alternative could be the use of predators (fish, water birds) to control *Lemna* growth. Predators should be chosen according to their human profit. As foreign species have a long and unfortunate record in places where they were introduced as control, a careful study of risks should be performed before using this method. Moreover, a predator must meet both two simultaneous requirements: reproduction rates enough high and limited efficiency of predating.

4) It is well known that: a) duckweeds reduce the environmental pollution if the plants are taken from the water before their decay returns the not desirable substances they have gathered, and b) duckweeds produce a large amount of high quality biomass. Therefore, *Lemna* cropping could be a mean of keeping the water quality high. Any direct human consumption should be preceded by the adequate elimination of salmonella and similar harmful bacteria from *Lemna* fronds. Moreover, a study of heavy metals concentration in water of the lake and on duckweed is also mandatory before human dietary use. Alternatively duckweeds could be used as raw material in pisciculture, avian or animal nutrition, or in fertilizers manufacturing.

There are many studies dealing with the use of *Lemna*. The step to be done now is to provide the current Lake Maracaibo region inhabitants with the appropriate knowledge and education to take **advantage** of having around them a huge source of raw material, which demands for its use just bending a little bit the waist.

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Appendix

The linearization process is based on the calculation of the Jacobian matrix in each one of the equilibrium points. For system [4] to [6] this matrix is given by:

$$J = \frac{\partial(X,Y,Z)}{\partial(x,y,z)} = \begin{bmatrix} \alpha_1 y - 2\alpha_2 x - z & \alpha_1 x & -x \\ -y & -1-x & 0 \\ \gamma z & 0 & \gamma x - \omega \end{bmatrix}. \qquad \text{[A-1]}$$

We limit ourselves to consider the general point P_G. The eigenvalues determinant is given by:

$$J_\lambda = \det\begin{pmatrix} -\frac{\alpha_2\omega}{\gamma} - \lambda & \alpha_1\frac{\omega}{\gamma} & -\frac{\omega}{\gamma} \\ -\frac{\gamma\beta}{\gamma+\omega} & -1-\frac{\gamma}{\omega}-\lambda & 0 \\ \gamma z^* & 0 & -\lambda \end{pmatrix} = 0,$$

with λ as the eigenvalue, and z^*, the equilibrium concentration of z. The characteristic polynomial is:

$$\lambda^3 + \lambda^2\left[\frac{\omega}{\gamma}(1+\alpha_2)+1\right] + \lambda\left[\frac{\alpha_2\omega}{\gamma}(\frac{\omega}{\gamma}+1) + \frac{\alpha_1\beta\omega}{\gamma+\omega} + \omega z^*\right] + \omega\left(\frac{\omega}{\gamma}+1\right)z^* = 0 \qquad \text{[A-2]}$$

This is, a $\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$ type polynomial. The Routh-Hurwitz criterion states that polynomial roots have real negative part if $a_1 > 0$; $a_3 > 0$; $a_1 a_2 - a_3 > 0$ (Stable system). The fulfillment of the first two conditions is verified by simple inspection, if $z^* > 0$. Moreover

$$a_1 a_2 - a_3 = \omega\left\{\left[\frac{\alpha_2}{\gamma}(\frac{\omega}{\gamma}+1) + \frac{\alpha_1\beta}{\gamma+\omega}\right]\right.$$

$\left[\frac{\omega}{\gamma}(1+\alpha_2)+1\right]+\frac{\alpha_2\omega}{\gamma}z^*\Big\}$ is positive if $z^* > 0$. Under the condition $\frac{\alpha_1\beta}{\gamma+\omega}=\frac{\alpha_2\omega}{\gamma}$ and by using the changes $\overline{x}=x-\frac{\omega}{\gamma}$, $\overline{y}=y-\frac{\alpha_2\omega}{\alpha_1\gamma}$, $\overline{z}=z$, system [4] to [6] can be written in compact form as $\dot{\overline{X}}=B\overline{X}+C$, where

$$\overline{X}=\begin{bmatrix}\overline{x}\\ \overline{y}\\ z\end{bmatrix},\ B=\begin{bmatrix}-\frac{\alpha_2\omega}{\gamma} & \frac{\alpha_1\omega}{\gamma} & -\frac{\omega}{\gamma}\\ -\frac{\alpha_2\omega}{\alpha_1\gamma} & -\frac{\alpha_1\beta\gamma}{\alpha_2\omega} & 0\\ 0 & 0 & 0\end{bmatrix}\text{ and}$$

$$C=\begin{bmatrix}-\alpha_1\overline{xy}-\alpha_2\overline{x}^2-\overline{xz}\\ -\overline{xy}\\ \gamma\overline{xz}\end{bmatrix}\qquad\text{[A-3].}$$

Notice that each component of vector C is a second degree polynomial in three variables and the same will happen with any vector that is obtained by means of $P^{-1}C$, where P is a non singular constant matrix. We will use this fact later on. On the other hand, the eigenvalues of B are:

$$\lambda_1=0\text{ and }\lambda_\pm=-\frac{A}{2}\pm\frac{\Delta}{2},\qquad\text{[A-4]}$$

where $A=\frac{\alpha_2\omega}{\gamma}+\frac{\alpha_1\beta\gamma}{\alpha_2\omega}$,

$$\Delta^2=\left(\frac{\alpha_2\omega}{\gamma}-\frac{\alpha_1\beta\gamma}{\alpha_2\omega}\right)^2-4\alpha_2\left(\frac{\omega}{\gamma}\right)^2.$$

We observe that $\lambda_\pm<0$ if $\Delta^2\geq 0$ and $\mathrm{Re}(\lambda_\pm)<0$ if $\Delta^2<0$. However, due to $\lambda_1=0$, we cannot reach a conclusion on stability immediately. We will pay attention to the case $\Delta^2\geq 0$ and, in order to obtain information concerning stability, a center manifold approach is followed. Our starting point consists in considering a change of variables based on a decomposition of matrix B, and this discussion is subdivided in two cases:

I) $\Delta^2>0$. In this case there exists a non singular matrix P, such that B can be decomposed as $B=PDP^{-1}$, where D is a diagonal matrix that contains in its diagonal the eigenvalues of B. In order to obtain P, we use the eigenvectors of B. The eigenvectors corresponding to the eigenvalue $\lambda_1=0$ are:

$$\left[-\frac{\alpha_1\beta}{\alpha_2(\alpha_2+\alpha_1\beta)}t,\ \frac{\alpha_2}{\alpha_1(\alpha_2+\alpha_1\beta)}t,t\right]^\tau,t\in\Re,\qquad\text{[A-5]}$$

and, the eigenvectors corresponding to $\lambda_\pm$ are:

$$\left[t,\left(\frac{\alpha_2}{\alpha_1}+\frac{\gamma}{\alpha_1\omega}\lambda_\pm\right)t,\ 0\right]^T,t\in\Re\qquad\text{[A-6]}$$

Now, taking $t=\alpha_2+\alpha_1\beta$ in [A-5], and $t=\alpha_1$ in [A-6], the matrix P is obtained as:

$$P=\begin{bmatrix}\alpha_1 & \alpha_1 & -\frac{\alpha_1\beta}{\alpha_2}\\ \frac{\gamma\lambda_+}{\omega}+\alpha_2 & \frac{\gamma\lambda_-}{\omega}+\alpha_2 & \frac{\alpha_2}{\alpha_1}\\ 0 & 0 & \alpha_2+\alpha_1\beta\end{bmatrix},$$

and its inverse is immediate.

Now, $B=PDP^{-1}$ being $D=\begin{bmatrix}\lambda_+ & 0 & 0\\ 0 & \lambda_- & 0\\ 0 & 0 & 0\end{bmatrix}$.

Next, we introduce a new variable $\overline{X}=\begin{bmatrix}\tilde{x}\\ \tilde{y}\\ \tilde{z}\end{bmatrix}$ through the change $\tilde{X}=P^{-1}\overline{X}$ and then (A-3) is written as:

$$\begin{bmatrix}\dot{\tilde{x}}\\ \dot{\tilde{y}}\\ \dot{\tilde{z}}\end{bmatrix}=\begin{bmatrix}\lambda_+ & 0 & 0\\ 0 & \lambda_- & 0\\ 0 & 0 & 0\end{bmatrix}\begin{bmatrix}\tilde{x}\\ \tilde{y}\\ \tilde{z}\end{bmatrix}+P^{-1}\tilde{C}\qquad\text{[A-7]}$$

where $\tilde{C}$ is the matrix C given in terms of $\tilde{x},\tilde{y}$ and $\tilde{z}$. Also, (A-7) can be decoupled as follows:

$$\begin{bmatrix} \dot{\tilde{x}} \\ \dot{\tilde{y}} \end{bmatrix} = \begin{bmatrix} \lambda_+ & 0 \\ 0 & \lambda \end{bmatrix} \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} + \begin{bmatrix} g_1(\tilde{x},\tilde{y},\tilde{z}) \\ g_2(\tilde{x},\tilde{y},\tilde{z}) \end{bmatrix} \qquad \text{[A-8]}$$

$$\dot{\tilde{z}} = 0.\tilde{z} + \alpha_1\gamma\left(\tilde{x} + \tilde{y} - \frac{\beta}{\alpha_2}\tilde{z}\right)\tilde{z}, \qquad \text{[A-9]}$$

where $g_1(\tilde{x},\tilde{y},\tilde{z})$ and $g_2(\tilde{x},\tilde{y},\tilde{z})$ are the two first components in the vector $P^{-1}\tilde{C}$. Let us now introduce the notation $g'(\cdot)$ to denote the Jacobians of the functions g_1 and g_2. We have, given that g_1 and g_2 are second degree polynomials in $\tilde{x},\tilde{y},\tilde{z}$ with zero independent term, that:

$g_1(0,0,0) = g_2(0,0,0) = 0$ and $g'_1(0,0,0) = g'_2(0,0,0) = 0$.

Therefore, the system [A-8]-[A-9] has a local center manifold at (0,0,0). Thus, there exist differentiable functions h_1, h_2 such that: $h_1(0) = h_2(0) = 0$, $h'_1(0) = h'_2(0) = 0$ and $\tilde{x}, \tilde{\gamma}$ are represented as $\tilde{x} = h_1(\tilde{z}), \tilde{\gamma} = h_2(\tilde{z})$. Since the system [A-8] is stable at the origin, the stability of the complete system [A-8]-[A-9] depends of the scalar equation [A-9]. A Taylor expansion, around $\tilde{z} = 0$, for the functions h_1 and h_2 allows us to write this equation as:

$$\dot{\tilde{z}} = \alpha_1\gamma\left[o(\tilde{z}^2) + o(\tilde{z}^2) - \frac{\beta}{\alpha_2}\tilde{z}\right]\tilde{z} = -\frac{\alpha_1\gamma\beta}{\alpha_2}\tilde{z}^2 + o(\tilde{z}^3).$$

Then (0,0,0) is a stable equilibrium point of the system [A-8]-[A-9].

II) $\Delta^2 = 0$ Here the eigenvectors corresponding to $\lambda_1 = 0$ do not change and, as before, are giving by [A-5]. The eigenvectors corresponding to the eigenvalue with multiplicity two, $\lambda_+ = \lambda_- \equiv \lambda = -\frac{1}{2}\left(\frac{\alpha_2\omega}{\gamma} + \frac{\alpha_1\beta\gamma}{\alpha_2\omega}\right)$ are:

$$\left[t,\ \frac{1}{2}\left(\frac{\alpha_2}{\alpha_1} - \frac{\beta\gamma^2}{\alpha_2\omega^2}\right)t,\ 0\right],\ t \in \Re \qquad \text{[A-10]}$$

In this case the space of vectors associated λ to have dimension one, and it is not possible to decompose B by using a diagonal matrix. Instead, we obtain a non singular matrix Q such that $B = QJQ^{-1}$, with $J = \begin{bmatrix} \lambda & 1 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & 0 \end{bmatrix}$. Let us consider the vector which is obtained by taking $t = 2$ in [A-10] and call it ν_1, we have $\nu_1 = \left[2, \frac{\alpha_2}{\alpha_1} - \frac{\beta\gamma^2}{\alpha_2\omega^2}, 0\right]^T$. After some computations, we obtain the set of vectors ν such that $(\lambda I - B)^2\nu = 0$ and $(\lambda I - B)\nu = \nu_1$, where I is the identity matrix, and this leads to:

$$\nu = \left[t \ \ \frac{\gamma}{\alpha_1\omega}\left(\frac{1}{2}\left(\frac{\alpha_2\omega}{\gamma} - \frac{\alpha_1\beta\gamma}{\alpha_2}\right)t - 2\right) \ \ 0\right]^T \qquad \text{[A-11]}$$

Let us consider the vector which is obtained by taking $t = 0$ in [A-11] and call it ν_2, we have $\nu_2 = \left[0 - \frac{2\gamma}{\alpha_1\omega} \ \ 0\right]^T$. Now, the matrix can be chosen as:

$$Q = \begin{bmatrix} 2 & 0 & \frac{-\alpha_1\beta}{\alpha_2} \\ \frac{\gamma}{\alpha_1\omega}\left(\frac{\alpha_2\omega}{\gamma} - \frac{\alpha_1\beta\gamma}{\alpha_2\omega}\right) & -\frac{2\gamma}{\alpha_1\omega} & \frac{\alpha_2}{\alpha_1} \\ 0 & 0 & \alpha_2 + \alpha_1\beta \end{bmatrix},$$

Hence, through the change $\tilde{X} = Q^{-1}\overline{X}$ the system [A-3] becomes in

$$\begin{bmatrix} \dot{\tilde{x}} \\ \dot{\tilde{y}} \\ \dot{\tilde{z}} \end{bmatrix} = \begin{bmatrix} \lambda & 0 & 0 \\ 0 & \lambda & 0 \\ 0 & 0 & 0 \end{bmatrix} \begin{bmatrix} \tilde{x} \\ \tilde{y} \\ \tilde{z} \end{bmatrix} + Q^{-1}\tilde{C} \qquad \text{[A-12]}$$

where now $\tilde{C}$ is the matrix C given in terms of $\tilde{x}, \tilde{y}$ and $\tilde{z}$. Also, [A-12] can be decoupled as:

$$\begin{bmatrix} \dot{\tilde{x}} \\ \dot{\tilde{y}} \end{bmatrix} = \begin{bmatrix} \lambda & 0 \\ 0 & \lambda \end{bmatrix} \begin{bmatrix} \tilde{x} \\ \tilde{y} \end{bmatrix} + \begin{bmatrix} f_1(\tilde{x},\tilde{y},\tilde{z}) \\ f_2(\tilde{x},\tilde{y},\tilde{z}) \end{bmatrix} \qquad \text{[A-13]}$$

$$\dot{\tilde{z}} = \gamma(\alpha_2 + \alpha_1\beta)\tilde{z}\left(2\tilde{x} - \frac{\alpha_1\beta}{\alpha_2}\tilde{z}\right), \qquad \text{[A-14]}$$

where $f_1(\tilde{x},\tilde{y},\tilde{z})$ and $f_2(\tilde{x},\tilde{y},\tilde{z})$ are the two first equations components in the vector

$Q^{-1}\tilde{C}$. Like case I) here f_1 and f_2 satisfy the conditions:

$f_1(0,0,0) = f_2(0,0,0) = 0$ and $f_1'(0,0,0) = f_2'(0,0,0) = 0$.

Therefore the system [A-13]-[A-14] has a local center manifold at (0,0,0), and now it is easy to observe that

$$\dot{\tilde{z}} = \gamma(\alpha_2 + \alpha_1\beta)\tilde{z}\left(2o(z^2) - \frac{\alpha_1\beta}{\alpha_2}\tilde{z}\right)$$

$$= -\frac{\alpha_1\beta\gamma(\alpha_2 + \alpha_1\beta)}{\alpha_2}\tilde{z}^2 + o(\tilde{z}^3).$$

Hence, (0,0,0) is a stable equilibrium point of the system [A-13]-[A-14].

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