

How do variations in water levels affect **Predator-prey interactions**

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RÉSUMÉ. Le niveau d'eau dans les rivières, les lacs et les réservoirs a une grande influence sur les interactions entre les projes et les prédateurs. En effet, l'augmentation du volume d'eau réduit la capture de la proie par le prédateur. Le même raisonnement s'applique lorsqu'il y a une diminution du volume d'eau, favorisant la capture de la proie par le prédateur. L'objectif de cet article est d'étudier les propriétés dynamiques d'un modèle prédateur-proie avec des prélèvements à taux constant non nul et soumis à des fluctuations du niveau d'eau dans un lac. Cette étude est importante pour comprendre le comportement et la dépendance des espèces à une variation saisonnière du niveau de l'eau. Des conditions ont été établies pour la coexistence et l'extinction des espèces. Les principaux résultats ont été illustrés par des simulations numériques. Les résultats de cette étude démontrent comment les variations du niveau d'eau peuvent affecter la répartition des espèces de poissons

ABSTRACT, Water level in rivers, lakes and reservoirs has great influence on the interactions between prey and predator fish. Indeed, the increase of the water volume hinders the capture of the prey by the predator. The same reasoning applies when there is a decrease in the volume of water, favoring the capture of the prey by the predator. The objective of this paper is to study the dynamical properties of a predator-prey model with nonzero constant rate prey harvesting and subject to fluctuating water level in a lake. This investigation is important to understand the behavior and dependence of species on a seasonal variation of water level. Conditions have been derived for for the coexistence and extinction of species. Main results have been illustrated using numerical simulations. The results of this study demonstrate how water level variations can affect the distribution of fish species

MOTS-CLÉS: Modèle prédateur-proie, stabilité, lac de Pareloup KEYWORDS: Predator-prey model, stability, Pareloup lac

1. Introduction.

Lac de Pareloup is a lake in Aveyron, France. It lies on the Lévézou plateau, 25 km south east of Rodez. This is the fifth largest hydroelectric reservoir by area in France having an area of 1260 hectares. Two interdependent fish species account as the most important species living this lake, They are the Roach species as prey (Gardon in French) and Pike species as predator (Brochet in French). The water level of Pareloup lake is regulated, mainly for hydroelectric purposes. The water level is lowered by increasing discharge in winter, when the consumption of electricity is highest. In the spring, snow melts refilling the lakes with the aid of the reduced discharge and the water level is usually kept quite constant over the summer until late summer. The management of this lake is of considerable ecological importance. Significant variations of the water level of the lake can have a strong impact on the persistence of some species. Indeed, when the water level is low, in winter, the contact between the predator and the prey is more frequent, and the predation increases. Conversely, when the water level is high, in the spring, its more difficult for the predator to find a prey and the predation decreases. In [4], the authors examine how seasonal variations in water level affect the outcome of a predator-prey interactions in Pareloup Lake. More recently, in [6] the authors assume that both species are subjected to harvesting and discuss the effects of water level and harvesting on the survival of the two species. All these studies demonstrate that the dynamics of the systems depends heavily on the fluctuation of the water level and give some valuable suggestions for saving the species and regulating populations when the ecological and environmental parameters are affected by periodic factors.

In this paper, we assume that the predator is not of commercial importance. The prey is continuously being harvested at a constant rate by a harvesting agency. The harvesting activity does not affect the predator population directly. It is obvious that the harvesting activity does reduce the predator population indirectly by reducing the availability of the prey to the predator. Let G(t) and B(t) are respectively the densities of the prey and predator at time t. We make the following assumptions:

- (A1) In the absence of predator, prey growing logistically with a growth rate γ_G .
- (A2) In the absence of prey, predator population declines exponentially.
- (A3) The predator need a quantity γ_B for his food, but he has access to a quantity of food depending on the water level equal

$$\frac{r}{H}\frac{G}{B+D},$$

where r is a positive constant, D measures the other causes of mortality outside the metabolism and predation and H is the water level of the lake. The minimum value of H is reached in autumn and the maximum value is attained during the spring. If

$$\frac{r}{H}\frac{G}{B+D} \ge \gamma_B,$$

then the predator will be satisfied with the quantity γ_B for his food. Otherwise, i.e if

$$\frac{r}{H}\frac{G}{B+D} \le \gamma_B,$$

the predator will content himself with

$$\frac{r}{H}\frac{G}{B+D}$$
.

Consequently, the quantity of food received by the predator is

$$\min\left(\frac{r}{H}\frac{G}{B+D},\gamma_B\right).$$

Considering the above basic assumptions we can now write the following dynamical system:

$$\begin{cases}
\frac{dG}{dt} = G(t) \left(\gamma_G - m_G G(t) \right) - \min \left(\frac{r}{H} \frac{G(t)}{B(t) + D}, \gamma_B \right) B(t) - Q, \\
\frac{dB}{dt} = -m_B B(t) + \min \left(\frac{r}{H} \frac{G(t)}{B(t) + D}, \gamma_B \right) B(t).
\end{cases}$$
[1]

where e is the conversion rate and Q represents the rate of harvesting (Q > 0).

The objective of this paper is to study the dynamical properties of the predator-prey model with constant harvesting. It will be better for us to determine how the water level and constant harvesting affect the dynamics of system (1).

Let B_0 , G_0 be respectively the initial density of the predator and prey with $B_0 > 0$ and $G_0 > 0$. We denote by

$$\begin{split} H_0 &= \max \left(\frac{r}{\gamma_B} \frac{G_0}{(B_0 + D)}, \frac{r \left(\left(\gamma_G + m_B \right)^2 - 4 m_G Q \right)}{4 m_G m_B \gamma_B D} \right), \\ H_1 &= \frac{e r}{2 m_G m_B D} \left(\gamma_G - \sqrt{\gamma_G^2 - 4 m_G Q} \right), \\ H_2 &= \frac{e r}{2 m_G m_B D} \left(\gamma_G + \sqrt{\gamma_G^2 - 4 m_G Q} \right). \end{split}$$

and we assume:

$$\frac{\gamma_G^2}{2m_G} \Big(\frac{B_0 + D}{B_0}\Big) < Q < min\Big(\frac{m_B D}{2e}, \frac{\gamma_G^2}{4m_G}\Big), \tag{2} \label{eq:2}$$

$$H > H_0 \tag{3}$$

Mathematical analysis and main result

Proposition 1 All the solutions of system (1) which initiate in R^2_+ are uniformly bounded.

Proof. See Appendix A.

To simplify our analysis, we rewrite system (1) in a simpler form. We prove the following result.

Proposition 2 Under hypothesis (3), we have $\frac{r}{H}G(t) < \gamma_B(B(t) + D), \ \forall t \geq 0.$

Proof. See Appendix B.

Consequently system (1) is reduced to the simple form

$$\begin{cases} \frac{dG}{dt} = G(t) \left(\gamma_G - m_G G(t) \right) - \frac{r}{H} \frac{G(t)B(t)}{B(t) + D} - Q, \\ \frac{dB}{dt} = e \frac{r}{H} \frac{G(t)B(t)}{B(t) + D} - m_B B(t). \end{cases}$$
 [4]

Local stability analysis of the steady states.

We now explore the existence and stability of boundary and positive equilibria of system (4)

Proposition 3 System (4) has the following equilibria:

$$-P_1=(G_1,0)$$
 , where $G_1=rac{\gamma_G-\sqrt{\gamma_G^2-4m_GQ}}{2m_G}$. $-P_2=(G_2,0)$, where $G_2=rac{\gamma_G+\sqrt{\gamma_G^2-4m_GQ}}{2m_G}$. and an interior equilibrium $P^*=(G^*,B^*)$, where

$$G^* = \frac{\left(\gamma_G - \frac{r}{H}\right) + \sqrt{\left(\gamma_G - \frac{r}{H}\right)^2 + 4m_G\left(\frac{m_B D}{e} - Q\right)}}{2m_G}, \ B^* = \frac{er}{m_B H}G^* - D.$$

It is easy to see that a necessary and sufficient condition for the existence of the interior equilibrium P^* is :

$$H_1 < H < H_2.$$
 [5]

3.1. Stability Analysis

Now we study the nature of these equilibria. The Jacobian matrix associated to (4) is given by

$$J\left(G,B\right) = \begin{pmatrix} \gamma_G - 2m_GG - \frac{r}{H}\frac{B}{B+D} & \frac{-r}{H}\frac{GD}{(B+D)^2} \\ \frac{er}{H}\frac{B}{B+D} & -m_B + \frac{er}{H}\frac{GD}{(B+D)^2} \end{pmatrix}.$$

We obtain the following results

• The axial equilibrium point P_1 is always unstable.

• The axial equilibrium point P_2 is stable if $H > H_2$ otherwise, it is a saddle point.

The proof is trivial and we omit it.

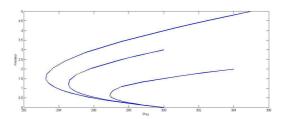


Figure 1. Extinction of the predator when $H > H_2 = 40$. The parameter values are : $\gamma_G = 7; m_G = 0.02; m_B = 7.5; e = 0.2; r = 50; D = 10; H = 60; Q = 300.$

Proposition 5 If condition (5) holds, and

$$H_* < H_1 < H_2$$

where $H_* = \frac{r}{\gamma_G}$, then the coexistence equilibrium P^* when it exists, it is locally asymptotic $\frac{r}{\gamma_G}$

Proof. See Appendix C.

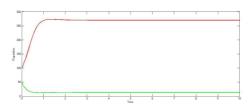


Figure 2. The densities of each species plotted against time when $H_1\,=\,2.85\,<\,H\,<\,$ $H_2 = 8.93$. The figure demonstrates the stability of the system (4) around the equilibrium (270.25, 13.24). The parameter values are : $\gamma_G = 7; m_G = 0.02; m_B = 5; e = 0.2; r = 0.02; m_B =$ 20; D = 30; H = 5; Q = 100.

Proposition 6 If condition (5) holds, and if

$$H_1 < H_* < H_2$$

then there exists \tilde{H} such that,

$$H_1 < \tilde{H} < H_2$$

and

- when $H_1 < H < \tilde{H}$, P^* is unstable.
- ullet when $ilde{H} < H < H_2, P^*$ is locally asymptotically stable.

Proof. See Appendix D.

4. Global stability of P^*

To investigate the global behavior of system (4) we first prove that system (4) around P^* has no nontrivial periodic solutions. The proof is based on an application of a divergence criterion [3]. Let $F(G,B)=\frac{1}{GB}$ Obviously F(G,B)>0 if G>0, B>0

$$f_1(G, B) = G(t) (\gamma_G - m_G G(t)) - \frac{r}{H} \frac{G(t)B(t)}{B(t) + D} - Q,$$

$$f_2(G, B) = e \frac{r}{H} \frac{G(t)B(t)}{B(t) + D} - m_B B(t),$$

and

$$\Delta(G, B) = \frac{\partial(Ff_1)}{\partial G} + \frac{\partial(Ff_2)}{\partial B}$$

We find that

$$\Delta(G,B) = \frac{1}{G^2 B} \left[-m_G G^2 + Q - \frac{er}{H} \frac{G^2 B}{(B+D)^2} \right] = \frac{1}{G^2 B} Tr J^*,$$

which is less than zero when the interior equilibrium is locally stable for all G > 0, B>0. As the solution is bounded, then by Bendixson-Dulac criterion, there will be no limit cycle in the first quadrant.

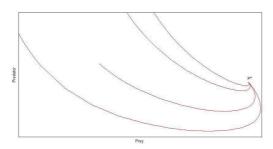


Figure 3. phase space trajectories corresponding to different initial levels.

Now, we are in a position to prove the following theorem.

Proposition 7 Existence and local stability of a positive interior equilibrium ensure that system (4) around P^* is globally asymptotically stable.

Proof. The proof is based on the following arguments:

- (a)-System (4) is bounded.
- (b)-The axial equilibrium P_1 is always an unstable saddle point and existence of positive equilibrium confirms that the axial equilibrium P_2 is also an unstable saddle point.
- (c)-Positive equilibrium P^* is LAS when $H_1 < H < H_2$.
- (d)-System (4) around P^* has no non-trivial periodic solutions.

Biological Implications:

Proposition 4 implies that Model (4) can have the-only prey population being locally stable at its equilibrium P_2 when the water level is high (Figure 1).

Proposition 5 implies that Model (4) can coexist at the equilibrium P^* if the water level is between two thresholds (Figures 2 and 3).

5. Existence of cycle limit

Proposition 8 If $H_1 < H < \tilde{H}$, then system (4) has at least one limit cycle.

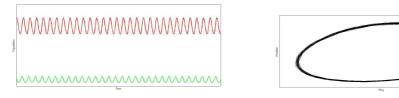


Figure 4. There is a limit cycle arrounding the unstable interior equilibrium point.

Proof. We have shown that all solutions are bounded and if $H_1 < H < \tilde{H}$, there are no asymptotically stable equilibrium point, we can deduce by Poincaré-Bendixson theorem [3] that there exists at least one periodic orbit (Figure 4).

6. Extinction of species

In this section, we prove a result on the extinction of the prey.

Proposition 9 If $H < H_1$, then the population of prey disappears.

Proof. From the first equation of system (4), we have

$$\frac{dG}{dt} = G(t)\left(\gamma_G - m_GG(t)\right) - \frac{r}{H}\frac{G(t)B(t)}{B(t) + D} - Q \leq G(t)\left(\gamma_G - m_GG(t)\right) - \frac{r}{H_1}\frac{G(t)B_0}{B_0 + D} - Q$$

$$\frac{dG}{dt} \le -m_G G^2 + \left(\gamma_G - \frac{2m_G Q}{\gamma_G} \frac{B_0}{B_0 + D}\right) G - Q$$

Using condition (2) we get

$$\frac{dG}{dt} < 0,$$

and this leads to the extinction of prey and subsequently that of predators.

7. Conclusion.

Based on the results of this work, it can be concluded that changes in water level have an impact on the distribution of species. By making some assumptions about biological parameters, we have reduced our model to a simple form. The boundedness of the system is established, which, in turn, implies that the system is biologically well posed. The mathematical analysis presented here, shows that if H is below the level H_1 , we will have the extinction of the species and beyond H_2 , we will have the extinction of the predators. It remains the level between H_1 and H_2 . Here we found two cases, the first when the level H_* is below H_1 , in this case the interior equilibrium point if it exist, it is locally asymptotically stable. The second case is when the H_* is between H_1 and H_2 , in which case we have shown numerically that there exists a \tilde{H} which changes the sign of the trace and hence the nature of P^* will change. Indeed, below \tilde{H} the trace is positive and P^* is unstable. Using Poincaré Bendixon's theorem we have proved the existence of at least one limit cycle around P^* . Above \tilde{H} , the trace becomes negative and therefore P^* is stable.

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Appendice A.

Proof of Proposition 1

We define a function

$$w = eG + B. ag{6}$$

The time derivative of (6) along the solutions of (1) is

$$\frac{dw}{dt} = e\frac{dG}{dt} + \frac{dB}{dt} = eG(\gamma_G - m_G G(t)) - Q - m_B B$$

then

$$\frac{dw}{dt} + m_B w \le eG(\gamma_G + m_B - m_G G(t)),$$

This implies that

$$\frac{dw}{dt} + m_B w \le \mu,$$

where
$$\mu=\frac{\left(\gamma_G+m_B\right)^2}{4m_G}.$$
 Applying the theory of differential inequalities [1], we obtain

$$0 \le w(G, B) \le \frac{\mu}{m_B} + e^{-m_B t} \left\{ w(G(0), B(0)) - \frac{\mu}{m_B} \right\},$$

and for $t \to \infty$, we have $0 \le w \le \frac{\mu}{m_B}$.

Hence all the solutions of (1) which initiate in R_+^2 are eventually confined in the region:

$$B = \left\{ (G, B) \in R_2^+ : w = \frac{\mu}{m_B} + \varepsilon, \forall \varepsilon > 0 \right\}.$$

Appendix B

Proof of Proposition 2

$$u(t) = \frac{r}{H}G(t) - \gamma_B(B(t) + D).$$

Note that u(0) < 0 by condition (3). It is claimed that u(t) < 0 for all t. If this were not the case, there exists $t_0>0$ such that : $u(t_0)=0$ and $\frac{du}{dt}(t_0)\geq 0$. The condition $u(t_0)=0$ implies that $B(t_0)=\frac{r}{\gamma_B H}G(t_0)-D$.

From (1), we get

$$\frac{du}{dt}(t_0) = \frac{r}{H}\frac{dG}{dt}(t_0) - \gamma_B \frac{dB}{dt}(t_0),$$

$$\frac{du}{dt}(t_0) = -\frac{r}{H}\left[\frac{r}{H} + e\gamma_B\right] \frac{B(t_0)}{B(t_0) + D}G(t_0) - \frac{r}{H}m_G\left(G(t_0)\right)^2 + \frac{r}{H}\left[\gamma_G + m_B\right]x(t_0) - \frac{r}{H}Q - m_B\gamma_BD.$$

It follows that

$$\frac{du}{dt}(t_0) \le -\frac{rm_G}{H} \left(G(t_0) \right)^2 + \frac{r}{H} \left[\gamma_G + m_B \right] G(t_0) - \frac{r}{H} Q - m_B \gamma_B D,$$

Condition (3) implies that $\frac{du}{dt}(t_0) < 0$ and we obtain a contradiction. This implies that u(t) < 0 for all $t \ge 0$.

Appendice C.

Proof of Proposition 5

The Jacobian matrix of (4) evaluated at the equilibrium P^* , is given by

$$J^* = \begin{pmatrix} -m_G G^* + \frac{Q}{G^*} & -\frac{r}{H} \frac{G^* D}{(B^* + D)^2} \\ \frac{er}{H} \frac{B^*}{B^* + D} & -\frac{er}{H} \frac{G^* B^*}{(B^* + D)^2} \end{pmatrix}.$$

Let $Det J^*$ and $Tr J^*$ be respectively the determinant and the trace associated to J^* , then

$$Det J^* = \frac{er}{H} \frac{B^*}{(B^* + D)^2} \left[m_G G^{2*} - Q + \frac{r}{H} \frac{G^* D}{B^* + D} \right],$$
$$= \frac{er}{H} \frac{B^*}{(B^* + D)^2} \left[m_G G^{2*} - Q + \frac{m_B D}{e} \right],$$

which is positive from the above conditions, and

$$TrJ^* = \frac{1}{G^*} \left(-m_G (G^*)^2 + Q - \frac{er}{H} \frac{(G^*)^2 B^*}{(B^* + D)^2} \right),$$
$$= \frac{1}{G^*} \left(2Q - \frac{m_B D}{e} - \left(\gamma_G - \frac{r}{H} \right) G^* - \frac{er}{H} \frac{(G^*)^2 B^*}{(B^* + D)^2} \right).$$

Condition (2) and $H > H^*$ give that $TrJ^* < 0$. Hence the equilibrium is locally asymptotically stable when $H_1 < H < H_2$.

Appendice D.

Proof of Proposition 6

Because of the difficulty that face us in searching the sign of the trace of J^* , we treat it numerically. We present in the figure 5 the graph of the trace as a function of the water level H where H is between the levels H_1 and H_2 .

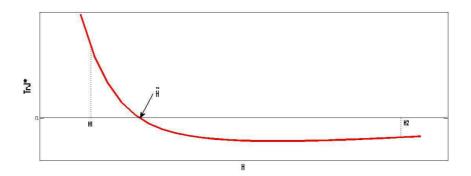


Figure 5. The trace against the level water H

According to this presentation, the trace at the point H_1 is positive and at the point H_2 it is negative. Moreover, between the levels H_1 and H_2 , it is decreasing. Thus, According to the Intermediate Value Theorem, there exists a $ilde{H}$ between H_1 and H_2 which annuls the trace and changes its sign.

We conclude that if $H_1 < H < \tilde{H}$, the trace is positive and therefore the interior equilibrium point P^* is unstable. Otherwise, if $\tilde{H} < H^2 < H_2$, the trace changes sign and becomes negative, and then P^* is locally asymptotically stable.