



Dynamical Behavior of a Delayed Predator-prey Model in Periodically Fluctuating Environments

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Abstract

In this paper we develop a non-autonomous predator-prey system with time delay to study the influence of water level fluctuations on the interactions between fish species living in an artificial lake. We derive persistence and extinction conditions of the species. Using coincidence degree theory, we determine conditions for which the system has at least one periodic solution. Numerical simulations are presented to illustrate theoretical results.

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1 Introduction

Changes in the water level of lakes, either natural or man-made, have a strong impact on the persistence of some fish species [1–5]. In [6], the authors examine how seasonal variations in water level affect the outcome of a predator-prey interactions in Pareloup lake in the south of France. The water level of Pareloup lake (area 12.6 km^2) 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. 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 [3,5]. 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, it is more difficult for the predator to find a prey and the predation decreases. Authors in [6] used the population densities of the Roach species (Gardon in French) as prey and the Pike species (Brochet in French) as the predator. Pike and Roach are the most important species in this lake. They studied the dynamic behavior of the following system of non-autonomous

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differential equations:

$$\begin{cases} \frac{dG}{dt}(t) = G(t) (\gamma_G - m_G G(t)) - \min(r(t) \frac{G(t)}{B(t) + D}, \gamma_B) B(t) \\ \frac{dB}{dt}(t) = e_B \min(r(t) \frac{G(t)}{B(t) + D}, \gamma_B) B(t) - m_B B(t) \end{cases} \tag{1}$$

subject to positive initial conditions

$$G(0) = G_0 > 0, \quad B(0) = B_0 > 0. \tag{2}$$

where the annual predation rate $(r(t))$ is a continuous periodic function of time, i.e. $r(t + 1) = r(t)$. The minimum value r_1 is reached in spring and the maximum value r_2 is attained during winter reflecting the high demand of electricity, γ_G and γ_B are respectively the maximum consumption rate of resource by prey and predator, e_B is the conversion rate, m_G and m_B are respectively the consumption rate of biomass by metabolism of prey and predator, D measures the other causes of mortality outside the predation. The historical origin and applicability of this model is discussed in detail in [6], the obtained results confirm the assumption that the water level fluctuations play a major role on the dynamic behavior of the predator-prey system. More recently, in [7], the authors investigated a more complex interaction among three species living in the Pareloup lake under seasonal succession, the authors showed that the system is permanent under some appropriate conditions and obtained sufficient conditions which ensure the existence of a positive 1-periodic solution. In [8], the author proposed a reaction-diffusion predator-prey model to predict the influence of variation of the water level on the persistence of positively periodic solutions. The existence of periodic solutions and their stability for a delayed version of (1) with delay in the prey specific growth term are studied in [9]. All these studies demonstrate that the dynamics of the system depends heavily on the fluctuation of the water level and gives some valuable suggestions for saving the two species and regulating populations when the ecological and environmental parameters are affected by periodic factors.

To achieve further understanding it is now essential to consider more general models. For example, we take into account the delay due to gestation and the time that takes for the predator to consume prey and reproduce their next generation [10, 11]. Indeed, the model we shall study in this paper takes the following form,

$$\begin{cases} \frac{dG}{dt}(t) = G(t) (\gamma_G - m_G G(t - \tau(t))) - \min(r(t) \frac{G(t)}{B(t) + D}, \gamma_B) B(t), \\ \frac{dB}{dt}(t) = e_B \min(r(t - \tau(t)) \frac{G(t - \tau(t))}{B(t - \tau(t)) + D}, \gamma_B) B(t) - m_B B(t), \end{cases} \tag{3}$$

subject to the initial conditions:

$$G_0(\theta) = \phi_1(\theta) > 0, \quad B_0(\theta) = \phi_2(\theta) > 0, \quad \theta \in [-\tau^M, 0], \tag{4}$$

where $\phi_i \in C([-\tau^M, 0], \mathbb{R}^+)$, $(i = 1, 2)$ are given functions and $\tau^M = \sup_{t \in \mathbb{R}_+} \tau(t)$ where $\tau(t)$ is a non negative and continuously differentiable periodic function with period 1.

The objective of this paper is to perform a qualitative analysis on this delayed system. It is well known by the fundamental theory of functional differential equations [10, 12, 13] that system (3) has a unique solution $X(t) = (G(t), B(t))$ satisfying initial conditions (4) and defined on $[0, \infty)$.

The organization of this paper is as follows. In Section 2, by employing the comparison Theorem and some analysis techniques, we discuss the uniform persistence and extinction of species. In Section 3, by using Gaines and Mawhin continuation Theorem of coincidence degree theory [14], sufficient conditions are derived for the existence of positive periodic solutions to system (3) with initial conditions (4). Lastly, two examples are given to show the feasibility of our main results by numerical simulations.

2 General non-autonomous case

In this section, we shall explore the dynamics of the non-autonomous predator-prey system (3) and present some results including the positive invariance, ultimate boundedness, permanence and predator extinction.

Let $\mathbb{R}_+^2 := \{(G, B) \in \mathbb{R}^2 \mid G \geq 0, B \geq 0\}$. For a bounded continuous function $g(t)$ on \mathbb{R} , we use the following notations:

$$g^M = \sup_{t \in \mathbb{R}} g(t), \quad g^L = \inf_{t \in \mathbb{R}} g(t).$$

Throughout this paper, we suppose that:

$$(H_1) : r_2 < \min\left(\frac{\gamma_B(B_0(\theta) + D)}{G_0(\theta)}, \frac{4m_B m_G D \gamma_B e^{-\gamma_G \tau^M}}{(\gamma_G + m_B)}\right), \quad \forall \theta \in [-\tau^M, 0],$$

$$(H_2) : e_B r_1 \left(\frac{\gamma_G - r_2}{m_G m_B}\right) \exp(-2\gamma_G) > D > 0.$$

Lemma 1. *Both the nonnegative and positive cones of \mathbb{R}^2 are positively invariant for (3).*

We omit the proof of Lemma 1 because it is similar to this of Lemma 1 of [9].

In the remainder of this paper, we only consider the solutions $(G(t), B(t))$ with positive initial values.

2.1 Dissipativeness and permanence

The concept of persistence plays an important role in mathematical ecology. When a system of interacting species is "persistent" in a suitable strong sense, it is quite sure that no species will go to an extinction in the future.

Definition 1. (Persistence:). System (3) is called weakly persistent if every solution $(G(t), B(t))$ satisfies two conditions:

- (i) $G(t) \geq 0, B(t) \geq 0, \forall t \geq \tau^M$.
- (ii) $\limsup_{t \rightarrow +\infty} G(t) > 0, \limsup_{t \rightarrow +\infty} B(t) > 0$.

System (3) is called be strongly persistent if every solution $(G(t), B(t))$ satisfies the following condition along with the first condition of the weak persistence:

- (iii) $\liminf_{t \rightarrow +\infty} G(t) > 0, \liminf_{t \rightarrow +\infty} B(t) > 0$.

Definition 2. (Permanence and non-permanence). The system (3) is said to be permanent if there are positive constants m , and M , with $0 < m \leq M$ such that

$$\min\{\liminf_{t \rightarrow +\infty} G(t), \liminf_{t \rightarrow +\infty} B(t)\} \geq m, \quad \max\{\limsup_{t \rightarrow +\infty} G(t), \limsup_{t \rightarrow +\infty} B(t)\} \leq M$$

for all solutions $(G(t), B(t))$ of system (3) with positive initial values. System (3) is said to be non-permanent if there is a positive solution $(G(t), B(t))$ of (3) and such that:

$$\min\{\liminf_{t \rightarrow +\infty} G(t), \liminf_{t \rightarrow +\infty} B(t)\} = 0.$$

To establish the persistence for the system (3), we need to recall the following Lemma,

Lemma 2. *If $a, b > 0$ and $\frac{dX}{dt} \leq (\geq) X(t)(a - bX(t))$, with $X(0) > 0$, then we have*

$$\limsup_{t \rightarrow \infty} X(t) \leq \frac{a}{b} \left(\liminf_{t \rightarrow \infty} X(t) \geq \frac{a}{b} \right).$$

The proof of this Lemma can be found in [15].

As the dependent variables are positive, from (3), we have

$$\frac{dG}{dt}(t) \leq \gamma_G G(t),$$

then

$$\frac{\frac{dG}{dt}(t)}{G(t)} \leq \gamma_G.$$

Integrating both sides of this inequality on the interval $[t - \tau(t), t]$ leads to

$$\frac{G(t)}{G(t - \tau(t))} \leq e^{\gamma_G \tau(t)} \leq e^{\gamma_G \tau^M},$$

it follows that

$$G(t - \tau(t)) \geq G(t) e^{-\gamma_G \tau^M}. \quad (5)$$

Also, we can easily see from (3) that

$$\frac{dG}{dt}(t) \leq G(t)(\gamma_G - m_G G(t - \tau(t))),$$

using (5) one obtains

$$\begin{aligned} \frac{dG}{dt}(t) &\leq G(t)(\gamma_G - m_G G(t) \exp(-\gamma_G \tau^M)), \\ &\leq m_G \exp(-\gamma_G \tau^M) G(t) \left(\frac{\gamma_G \exp(\gamma_G \tau^M)}{m_G} - G(t) \right). \end{aligned}$$

A standard comparison argument shows that

$$\limsup_{t \rightarrow \infty} G(t) \leq \frac{\gamma_G}{m_G} \exp(\gamma_G \tau^M) := M_1. \quad (6)$$

Thus for arbitrary $\varepsilon > 0$, there exist a positive real number T_1 such that

$$G(t) \leq M_1 + \varepsilon \quad \forall t > T_1 + \tau^M. \quad (7)$$

According to the second equation of system (3) and using the fact that :

$$B(t - \tau(t)) \geq B(t) \exp\{(-e_{Br_2}(M_1 + \varepsilon)/D)\tau^M\} \quad \text{for } t > T_1 + \tau^M,$$

we get

$$\begin{aligned} \frac{dB}{dt}(t) &\leq B(t) \left(e_{Br_2} \frac{(M_1 + \varepsilon)}{B(t) \exp\{(-e_{Br_2}(M_1 + \varepsilon)/D)\tau^M\} + D} - m_B \right) \\ &\leq \frac{B(t)}{B(t) \exp\{(-e_{Br_2}(M_1 + \varepsilon)/D)\tau^M\} + D} \\ &\quad (e_{Br_2}(M_1 + \varepsilon) - m_B D - m_B \exp\{(-e_{Br_2}(M_1 + \varepsilon)/D)\tau^M\} B(t)). \end{aligned}$$

Also using a standard comparison argument, we obtain

$$\limsup_{t \rightarrow +\infty} B(t) \leq \frac{e_{Br_2}(M_1 + \varepsilon) - m_B D}{m_B} \exp\{(e_{Br_2}(M_1 + \varepsilon)/D)\tau^M\}.$$

By setting $\varepsilon \rightarrow 0$ in above inequality, we get

$$\limsup_{t \rightarrow +\infty} B(t) \leq \frac{e_{Br_2}M_1 - m_B D}{m_B} \exp\{(e_{Br_2}M_1/D)\tau^M\} := M_2. \tag{8}$$

Note that the condition (H_2) implies that $M_2 > 0$. Therefore, there exists a $T_2 > T_1 + \tau^M$ such that

$$B(t) \leq M_2 + \varepsilon \quad \text{for } t > T_2. \tag{9}$$

The above results can be summarized into the following Theorem.

Theorem 3. *If (H_1) and (H_2) hold, then any solution of (3) starting from the interior of the first quadrant satisfies the following inequalities:*

$$\limsup_{t \rightarrow \infty} G(t) \leq \frac{\gamma_G}{m_G} \exp(\gamma_G \tau^M) := M_1$$

$$\limsup_{t \rightarrow +\infty} B(t) \leq \frac{e_{Br_2}M_1 - m_B D}{m_B} \exp\{(e_{Br_2}M_1/D)\tau^M\} := M_2.$$

Before giving the strongly persistence of system (3), we give the following result.

Lemma 4. *If (H_1) holds, we have for all $t \geq 0$,*

$$r_2 G(t) \leq \gamma_B(B(t) + D).$$

Proof. See Appendix

Consequently under hypothesis (H_1) , system (3) is reduced to the simple form

$$\begin{cases} \frac{dG}{dt}(t) = G(t)(\gamma_G - m_G G(t - \tau(t))) - r(t) \frac{G(t)}{B(t) + D} B(t), \\ \frac{dB}{dt}(t) = e_{Br}(t - \tau(t)) \frac{G(t - \tau(t))}{B(t - \tau(t)) + D} B(t) - m_B B(t). \end{cases} \tag{10}$$

Now, we come back to the proof of the (strongly) persistence of system (10) (which is equivalent to system (3) under hypothesis (H_1)).

According to the first equation of system (10), we have

$$\frac{dG}{dt}(t) \geq G(t)(\gamma_G - r_2 - m_G G(t - \tau(t))),$$

using the fact that

$$G(t - \tau(t)) \leq G(t) \exp(-(\gamma_G - r_2 - m_G(M_1 + \varepsilon))\tau^L) \text{ for all } t > \tau^M,$$

we get

$$\begin{aligned} \frac{dG}{dt}(t) &\geq G(t)(\gamma_G - r_2 - m_G \exp(-(\gamma_G - r_2 - m_G(M_1 + \varepsilon))\tau^L))G(t) \\ &\geq m_G \exp(-(\gamma_G - r_2 - m_G(M_1 + \varepsilon))\tau^L)G(t) \\ &\quad \left(\frac{(\gamma_G - r_2) \exp((\gamma_G - r_2 - m_G(M_1 + \varepsilon))\tau^L)}{m_G} - G(t) \right), \end{aligned}$$

it follows that

$$\liminf_{t \rightarrow +\infty} G(t) \geq \frac{\gamma_G - r_2}{m_G} \exp((\gamma_G - r_2 - m_G(M_1 + \varepsilon))\tau^L).$$

By setting $\varepsilon \rightarrow 0$ in above inequality, we have

$$\liminf_{t \rightarrow +\infty} G(t) \geq \frac{\gamma_G - r_2}{m_G} \exp((\gamma_G - r_2 - m_G M_1) \tau^L) := m_1. \quad (11)$$

Therefore, there exists enough large $T_3 > T_2$ such that for $t > T_3$,

$$G(t) \geq m_1 - \varepsilon. \quad (12)$$

Substituting (12) into the second equation of system (10) and that for any $t > T_3 + \tau$,

$$\frac{dB}{dt}(t) \geq B(t) \left(e_{Br_1} \frac{(m_1 - \varepsilon)}{B(t - \tau(t)) + D} - m_B \right),$$

using the fact that:

$$B(t - \tau(t)) \leq B(t) \exp(m_B \tau^M),$$

we get

$$\begin{aligned} \frac{dB}{dt}(t) &\geq B(t) \left(e_{Br_1} \frac{(m_1 - \varepsilon)}{B(t) \exp(m_B \tau^M) + D} - m_B \right), \\ &\geq \frac{B(t)}{B(t) \exp(m_B \tau^M) + D} (e_{Br_1} (m_1 - \varepsilon) - m_B D - m_B \exp(m_B \tau^M) B(t)). \end{aligned}$$

Also using a standard comparison argument we can get that

$$\liminf_{t \rightarrow +\infty} B(t) \geq \frac{e_{Br_1} (m_1 - \varepsilon) - m_B D}{m_B} \exp(-m_B \tau^M).$$

Setting $\varepsilon \rightarrow 0$ in above inequality, we obtain

$$\liminf_{t \rightarrow +\infty} B(t) \geq \frac{e_{Br_1} m_1 - m_B D}{m_B} \exp(-m_B \tau^M) := m_2, \quad \text{provided } r_1 > \frac{m_B D}{e_B m_1}. \quad (13)$$

The above results can be summarized into the following Theorem.

Theorem 5. *In addition to (H_1) , assume further that*

$$r_1 > \frac{m_B D}{e_B m_1} \quad (H_3)$$

holds. Then system (3) is strongly persistent.

Remark 1. Theorem 5 along with Definition 1 ensure that system (3) is strongly persistent provided the conditions (H_1) and (H_3) hold. Since conditions of the Theorem 5 also ensure that

$$\limsup_{t \rightarrow +\infty} G(t) > 0, \quad \limsup_{t \rightarrow +\infty} B(t) > 0,$$

the system (3) is weakly persistent under the conditions of the Theorem 5.

Consequently, combining (6), (8), (11) with (13), we arrive at the following result:

Corollary 6. *Under conditions (H_1) - (H_3) , permanence coexistence holds for the system (3).*

Concerned with the extinction of the predator species, we have

Proposition 7. Assume that

$$r_2 \leq \frac{m_B D}{e_B M_1}. \tag{H_0}$$

Then the predator species in system (10) will be driven to extinction.

Proof. From the last equation of system (10), we obtain

$$\frac{dB}{dt} \leq B(t) \left(\frac{e_B r_2 M_1}{D} - m_B \right),$$

and so,

$$B(t) \leq B_0 e^{((\frac{e_B r_2 M_1}{D} - m_B)t)}.$$

From condition (H₀) in Proposition 7, it immediately follows that $\lim_{t \rightarrow \infty} B(t) = 0$.

3 The model with periodic coefficients

It is well known that the existence of periodic solutions has been one of the most attracting topics in the qualitative theory of retarded functional differential equations for its significance in various engineering and natural problems. So, in this section, we confine ourselves to the case when the parameter $r(t)$ in system (3) is 1-periodic and we obtain sufficient conditions for the existence of a positive periodic solution of the system (3) by using the method of coincidence degree theory [14]. The periodic oscillation of the parameter seems reasonable in view of seasonal factors.

We first make the following preparations. Let \mathbb{X} and \mathbb{Y} be two Banach spaces. Define an abstract equation in \mathbb{X} ,

$$Lu = Nu, \tag{14}$$

where $L : DomL \subset \mathbb{X} \rightarrow \mathbb{Y}$ is a linear mapping and $N : \mathbb{X} \rightarrow \mathbb{Y}$ is a continuous mapping. The mapping L is called a Fredholm mapping of index zero if

$$dimkerL = codimImL < +\infty$$

and ImL is closed in \mathbb{Y} . If L is a Fredholm mapping of index zero, then there exist continuous projectors $P : \mathbb{X} \rightarrow \mathbb{X}$ and $Q : \mathbb{Y} \rightarrow \mathbb{Y}$ such that $ImP = kerL$ and $ImL = kerQ = Im(I - Q)$. It follows that $L|_{DomL \cap KerP} : (I - P)\mathbb{X} \rightarrow ImL$ is invertible. We denote the inverse of that map by K_p . If Ω is an open bounded subset of \mathbb{X} , the mapping N is called L -compact on $\overline{\Omega}$ if the mapping $QN : \overline{\Omega} \rightarrow \mathbb{Y}$ is continuous, $QN(\overline{\Omega})$ is bounded and $K_p(I - Q)N : \overline{\Omega} \rightarrow \mathbb{X}$ is compact. Since ImQ is isomorphic to $kerL$, there exists an isomorphism $J : ImQ \rightarrow kerL$.

Let Ω be an open bounded subset of \mathbb{X} with closure $\overline{\Omega}$ and $f \in C^1(\Omega, \mathbb{R}^n) \cap C(\Omega, \mathbb{R}^n)$. For $x \in \Omega$, let $J_f(x)$ denotes the Jacobian determinant of f at x and S_f be a set of all critical points of f , i.e $S_f = \{x \in \Omega : J_f(x) = 0\}$.

Definition 3. For $y \in \mathbb{R}^n \setminus f(\partial\Omega \cup S_f)$, i.e., y is a regular point of f , the degree of f at y is defined as

$$deg\{f, \Omega, y\} = \sum_{x \in f^{-1}(y)} sgnJ_f(x),$$

with the agreement that the previous sum is zero if $f^{-1}(y) = \emptyset$.

In our proof of the existence of a positive periodic solution of (3), we also need the following Lemma.

Lemma 8. (Continuation theorem [14], p.40)

Let \mathbb{X} and \mathbb{Y} be two Banach spaces and L be a Fredholm mapping of index zero. Assume that $N : \overline{\Omega} \rightarrow \mathbb{Y}$ is L -compact on $\overline{\Omega}$ with Ω is open and bounded in \mathbb{X} . Furthermore assume:

1. for each $\lambda \in (0, 1)$, every solution of $Lx = \lambda Nx$ is such that $x \notin \partial\Omega \cap \text{Dom}L$,
2. $QNx \neq 0$ for each $x \in \partial\Omega \cap \ker L$,
3. $\deg\{JQN, \Omega \cap \ker L, 0\} \neq 0$.

Then the operator equation $Lx = Nx$ has at least one solution in $\text{Dom}L \cap \overline{\Omega}$.

According to Lemma 8, we firstly construct a Banach space \mathbb{X} , which is composed of all periodic vector functions. By defining two mappings L and N , the system (3) is rewritten into an abstract equation $Lu = Nu$. The Lemma 8 shows that under conditions (1–3), the abstract equation $Lu = Nu$ has at least one solution, which belongs to a bounded open subset of the Banach space \mathbb{X} . Therefore, the system (3) has at least one periodic solution. The key of this method is to construct the bounded open subset of Banach space \mathbb{X} such that it can meet the conditions of the Lemma.

We are ready to state and prove our main Theorem.

Theorem 9. Under conditions (H_1) and (H_2) , the system (3) has at least one positive 1-periodic solution.

Proof. Making the change of variables

$$G(t) = \exp(u_1(t)), \quad B(t) = \exp(u_2(t)),$$

and taking into account Lemma 4, system (3) is reformulated as

$$\begin{cases} \frac{du_1}{dt}(t) = \gamma_G - m_G \exp(u_1(t - \tau(t))) - r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D}, \\ \frac{du_2}{dt}(t) = e_{Br}(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t))) + D} - m_B. \end{cases} \quad (15)$$

Let

$$\mathbb{X} = \mathbb{Y} = \{u = (u_1, u_2)^T \in C(\mathbb{R}, \mathbb{R}^2) : u_1(t+1) = u_1(t), u_2(t+1) = u_2(t), \text{ for all } t \in \mathbb{R}\}$$

and

$$\|u\| = \max_{t \in [0,1]} |u_1(t)| + \max_{t \in [0,1]} |u_2(t)|, \quad u \in \mathbb{X} \text{ (or } \mathbb{Y}\text{)}.$$

It is not difficult to show that \mathbb{X}, \mathbb{Y} are both Banach spaces when they are endowed with the above norm $\|\cdot\|$.

Let $L : \text{Dom}L \cap \mathbb{X} \rightarrow C(\mathbb{R}, \mathbb{R}^2)$ be the operator

$$Lu = \dot{u}, \quad (\dot{u} = \frac{du}{dt}),$$

where $\text{Dom}L = C^1(\mathbb{R}, \mathbb{R}^2)$ and $N : \mathbb{X} \rightarrow \mathbb{X}$ is the mapping defined by

$$N \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} N_1 \\ N_2 \end{pmatrix} = \begin{pmatrix} \gamma_G - m_G \exp(u_1(t - \tau(t))) - r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D} \\ e_{Br}(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t))) + D} - m_B \end{pmatrix}.$$

Define the projectors P and Q as

$$Pu = Qu = \begin{pmatrix} \int_0^1 u_1(s) ds \\ \int_0^1 u_2(s) ds \end{pmatrix} \quad u \in \mathbb{X} = \mathbb{Y}.$$

Then

$$\ker L = \{u \in \mathbb{X} \mid u = c \in \mathbb{R}^2\}$$

and

$$\text{Im}L = \{u \in \mathbb{Y} \mid \int_0^1 u_1(s)ds = \int_0^1 u_2(s)ds = 0\},$$

is closed in \mathbb{X} and $\dim \ker L = \text{codim Im}L = 2$. Since $\text{Im}L$ is closed in \mathbb{X} , L is a Fredholm mapping of index zero. It is easy to show that P, Q are continuous projections such that

$$\text{Im}P = \text{Ker}L, \text{Im}L = \text{Ker}Q = \text{Im}(I - Q).$$

Furthermore, the generalized inverse (to L) $K_p : \text{Im}L \rightarrow \text{Dom } L \cap \ker P$ exists and is given by

$$K_p u = \begin{pmatrix} \int_0^t u_1(s) ds - \int_0^1 \int_0^t u_1(s) ds dt \\ \int_0^t u_2(s) ds - \int_0^1 \int_0^t u_2(s) ds dt \end{pmatrix}.$$

Indeed, corresponding to the operator equation $L(u) = v$, it follows that

$$\frac{du}{dt} = v. \tag{16}$$

Integrating (16) over the interval $[0, t]$ leads to

$$u(t) = u(0) + \int_0^t v(s) ds. \tag{17}$$

Integrating again both sides of this equality on the interval $[0, 1]$, we obtain,

$$0 = u(0) + \int_0^1 \int_0^t v(s) ds,$$

then

$$u(0) = - \int_0^1 \int_0^t v(s) ds.$$

Hence

$$u(t) = \int_0^t v(s) ds - \int_0^1 \int_0^t v(s) ds.$$

Thus

$$QN u = \begin{pmatrix} \int_0^1 \left(\gamma_G - m_G \exp(u_1(t - \tau(t))) - r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D} \right) dt \\ \int_0^1 \left(e_{Br}(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t))) + D} - m_B \right) dt \end{pmatrix},$$

and

$$K_p(I - Q)Nu = \begin{pmatrix} \int_0^t N_1(s) ds - \int_0^1 \int_0^t N_1(s) ds dt - (t - \frac{1}{2}) \int_0^1 N_1(t) dt \\ \int_0^t N_2(s) ds - \int_0^1 \int_0^t N_2(s) ds dt - (t - \frac{1}{2}) \int_0^1 N_2(t) dt \end{pmatrix}.$$

Obviously, QN and $K_p(I - Q)N$ are continuous. Since \mathbb{X} is a Banach space, using the Arzela-Ascoli Theorem, it is easy to show that $K_p(I - Q)N(\overline{\Omega})$ is compact for any open bounded set $\Omega \subset \mathbb{X}$. Moreover, $QN(\overline{\Omega})$ is bounded. Thus, N is L -compact on $\overline{\Omega}$ with any open bounded set $\Omega \subset \mathbb{X}$.

Now we are in the position to search for an appropriate open and bounded subset Ω for the application of continuation Theorem. For the operator equation $Lu = \lambda Nu, \lambda \in (0, 1)$, we have

$$\begin{cases} \frac{du_1}{dt}(t) = \lambda \left(\gamma_G - m_G \exp(u_1(t - \tau(t))) - r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D} \right), \\ \frac{du_2}{dt}(t) = \lambda \left(e_{Br}(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t))) + D} - m_B \right). \end{cases} \tag{18}$$

Assume that $u = (u_1, u_2)^T \in \mathbb{X}$ is an arbitrary solution of system (18) for a certain $\lambda \in (0, 1)$. Integrating both sides of (18) over the interval $[0, 1]$, we obtain

$$\begin{cases} \gamma_G = \int_0^1 \left(m_G \exp(u_1(t - \tau(t))) + r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D} \right) dt, \\ m_B = \int_0^1 \left(e_{Br}(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t))) + D} \right) dt. \end{cases} \tag{19}$$

It follows from (18) and (19) that

$$\int_0^1 \left| \frac{d}{dt} u_1(t) \right| dt \leq \lambda \left(\int_0^1 \gamma_G dt + \int_0^1 \left(m_G \exp(u_1(t - \tau(t))) + r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D} \right) dt \right), \tag{20}$$

$$\leq 2\gamma_G.$$

$$\int_0^1 \left| \frac{d}{dt} u_2(t) \right| dt \leq \lambda \left(\int_0^1 m_B dt + \int_0^1 e_{Br}(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t))) + D} dt \right), \tag{21}$$

$$\leq 2m_B.$$

Note that since $u \in \mathbb{X}$, there exist $\zeta_i, \eta_i \in [0, 1], i \in [1, 2]$, such that

$$\begin{aligned} u_1(\zeta_1) &= \min_{t \in [0,1]} u_1(t), & u_1(\eta_1) &= \max_{t \in [0,1]} u_1(t), \\ u_2(\zeta_2) &= \min_{t \in [0,1]} u_2(t), & u_2(\eta_2) &= \max_{t \in [0,1]} u_2(t). \end{aligned} \tag{22}$$

From (22) and the first equation of (19), we have

$$\gamma_G \geq \int_0^1 m_G \exp(u_1(\zeta_1)) dt \geq m_G \exp(u_1(\zeta_1)),$$

which implies that

$$u_1(\zeta_1) \leq \ln\left(\frac{\gamma_G}{m_G}\right) := L_1. \tag{23}$$

Then, from (22) and (20), we get

$$u_1(t) \leq u_1(\zeta_1) + \int_0^1 \left| \frac{d}{dt} u_1(t) \right| dt < \ln\left(\frac{\gamma_G}{m_G}\right) + 2\gamma_G := K_1. \tag{24}$$

On the other hand, from (22) and the first equation of (19), we also have

$$\begin{aligned} \gamma_G &= \int_0^1 \left(m_G \exp(u_1(t - \tau(t))) + r(t) \frac{\exp(u_2(t))}{\exp(u_2(t)) + D} \right) dt, \\ &\leq \int_0^1 m_G \exp(u_1(\eta_1)) dt + r_2, \end{aligned}$$

which implies that

$$u_1(\eta_1) \geq \ln\left(\frac{\gamma_G - r_2}{m_G}\right) := l_1 \tag{25}$$

and along with (21), we obtain

$$u_1(t) \geq u_1(\eta_1) - \int_0^1 \left| \frac{d}{dt} u_1(t) \right| dt > \ln\left(\frac{\gamma_G - r_2}{m_G}\right) - 2\gamma_G := K_2,$$

which, together with (24), leads to

$$\max_{t \in [0,1]} |u_1(t)| \leq \max\{|K_1|, |K_2|\} := R_1. \tag{26}$$

From (22) and the second equation of (19), we have

$$\begin{aligned} m_B &\leq \int_0^1 e_B r(t - \tau(t)) \frac{\exp(u_1(t - \tau(t)))}{\exp(u_2(t - \tau(t)))} dt, \\ &\leq \frac{e_B \gamma_G r_2}{m_G} \exp(2\gamma_G) \int_0^1 \frac{1}{\exp(u_2(\zeta_2))} dt, \end{aligned}$$

which implies that

$$u_2(\zeta_2) \leq \ln\left(\frac{e_B \gamma_G r_2}{m_G m_B}\right) + 2\gamma_G := L_2, \tag{27}$$

and along with (20), we obtain

$$u_2(t) \leq u_2(\zeta_2) + \int_0^1 \left| \frac{d}{dt} u_2(t) \right| dt < \ln\left(\frac{e_B \gamma_G r_2}{m_G m_B}\right) + 2(\gamma_G + m_B) := K_3. \tag{28}$$

The second equation of (19), also produces

$$m_B \geq e_B r_1 \left(\frac{\gamma_G - r_2}{m_G}\right) \exp(-2\gamma_G) \int_0^1 \frac{1}{\exp(u_2(\eta_2)) + D} dt,$$

which implies that

$$u_2(\eta_2) \geq \ln\left(e_B r_1 \left(\frac{\gamma_G - r_2}{m_G m_B}\right) \exp(-2\gamma_G) - D\right) := l_2, \tag{29}$$

and along with (21), we get

$$u_2(t) \geq u_2(\eta_2) - \int_0^1 \left| \frac{d}{dt} u_2(t) \right| dt < \ln\left(e_B r_1 \left(\frac{\gamma_G - r_2}{m_G m_B}\right) \exp(-2\gamma_G) - D\right) - 2m_B := K_4,$$

which, together with (28), leads to

$$\max_{t \in [0,1]} |u_2(t)| \leq \max\{|H_3|, |H_4|\} := R_2. \tag{30}$$

Obviously, R_1 and R_2 are both independent of λ .

Next, for $v \in [0, 1]$, we consider the following algebraic equations:

$$\begin{cases} \gamma_G - m_G \exp(u_1) - \bar{r} \frac{v \exp(u_2)}{\exp(u_2) + D} = 0 \\ e_B \bar{r} \frac{\exp(u_2)}{\exp(u_2 + D)} - m_B = 0, \end{cases} \tag{31}$$

where $(u_1, u_2)^T \in \mathbb{R}^2$. By the similar argument of (23), (25), (27) and (29), we can derive the solutions $(u_1, u_2)^T$ of (31) that satisfy

$$l_1 \leq u_1 \leq L_1, \quad l_2 \leq u_2 \leq L_2. \tag{32}$$

Denote $R = R_1 + R_2 + R_3$, where $R_3 > 0$ is taken sufficiently large such that $R_3 \geq |l_1| + |L_1| + |l_2| + |L_2|$, we define

$$\Omega = \{u \in \mathbb{X} : \|(u_1, u_2)^T\| < R\}.$$

Now we check the conditions of Lemma 8.

(1)- From (26) and (30), one can see that for each $\lambda \in [0, 1]$ and $u \in \partial\Omega \cap \text{Dom}L$, $Lu \neq \lambda u$.

(2)- When $(u_1, u_2)^T \in \partial\Omega \cap \ker L = \partial\Omega \cap \mathbb{R}^2$, then $u = (u_1, u_2)^T$ is a constant vector in \mathbb{R}^2 with $\| (u_1, u_2)^T \| = |u_1| + |u_2| = R$. If

$$QN \begin{pmatrix} u_1 \\ u_2 \end{pmatrix} = \begin{pmatrix} \gamma_G - m_G \exp(u_1) - \bar{r} \frac{\exp(u_2)}{\exp(u_2)+D} \\ e_B \bar{r} \frac{\exp(u_1)}{\exp(u_2)+D} - m_B \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

then $(u_1, u_2)^T$ is the constant solution of system (31) with $v = 1$. From (32), $\| (u_1, u_2)^T \| < R$. This contradiction implies that for each $(u_1, u_2)^T \in \partial\Omega \cap \ker L$, $QNu \neq 0$.

(3)- To compute the Brouwer degree, let us consider the homotopy

$$H_v(u) = vQN(u) + (1 - v)G(u) \quad \text{for } v \in [0, 1],$$

where

$$G(u) = \begin{pmatrix} \gamma_G - m_G \exp(u_1) \\ e_B \bar{r} \frac{\exp\{u_1\}}{\exp(u_2)+D} - m_B \end{pmatrix}.$$

From (32), it is easy to show that $0 \notin H_v(\partial\Omega \cap \text{Ker} L)$ for $v \in [0, 1]$. Moreover, one can easy show that the algebraic equation $G(u) = 0$ has a unique solution $(u_1^*, u_2^*) = (\ln(\frac{\gamma_G}{m_G}), \ln(\frac{e_B \bar{r} \gamma_G}{m_B m_G} - D))$ in \mathbb{R}^2 . By the invariance property of homotopy, we have

$$\deg(JQN, \Omega \cap \text{Ker}L, 0) = \deg(QN, \Omega \cap \text{Ker}L, 0) = \deg(G, \Omega \cap \text{Ker}L, 0).$$

Thus,

$$\begin{aligned} \deg(G, \Omega \cap \text{Ker}L, 0) &= \underset{(u_1^*, u_2^*) \in QN^{-1}\{0\}}{\text{sgn}} \det |G(u_1^*, u_2^*)| \\ &= \text{sgn} \begin{vmatrix} -m_G \exp\{u_1^*\} & 0 \\ \frac{e_B \bar{r} \exp\{u_1^*\}}{\exp\{u_2^*\}+D} & -\frac{e_B \bar{r} \exp\{u_1^*+u_2^*\}}{(\exp(u_2^*)+D)^2} \end{vmatrix} \\ &= 1 \neq 0. \end{aligned}$$

By now we have proved that Ω satisfies all requirements of previous Lemma. Thus system (15) has at least one 1-periodic solution. As a consequence, system (3) has at least one positive 1-periodic solution.

Remark 2. We established existence which leads to a criterion of species survival, it is based on the values of the function r which depends directly on the level water of the lake. The result given by Theorem 9 has an interesting ecological interpretation, since it illustrates that suitable levels water can make benefits in terms of survival of the species.

4 Numerical simulations

We consider here two examples to implement the theoretical results.

Example 1. As a first example, we consider system (3) with the parameter values: $r(t) = 0.6 + 0.2\cos(2\pi t)$, $\tau(t) = 0.3$, $\gamma_G = 3$, $m_G = 0.3$, $m_B = 0.4$, $D = 0.5$, $e_B = 1$, $\gamma_B = 40$, with initial values:

(1) $G(\theta) = 18$, $B(\theta) = 0.3$,

(2) $G(\theta) = 22$, $B(\theta) = 0.35$,

(3) $G(\theta) = 27$, $B(\theta) = 0.8$.

for all $\theta \in [-\tau^M, 0]$.

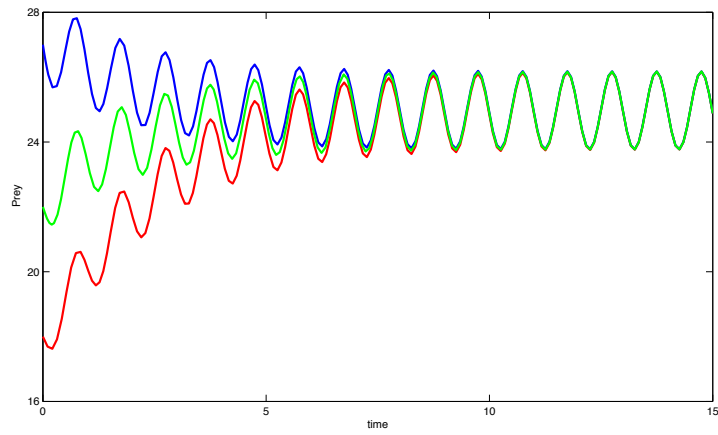


Fig. 1 Variation of preys with three different initial values.

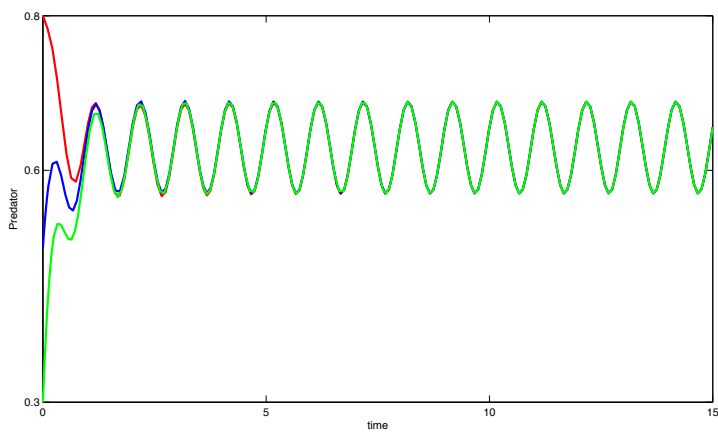


Fig. 2 Variation of predators with three different initial values.

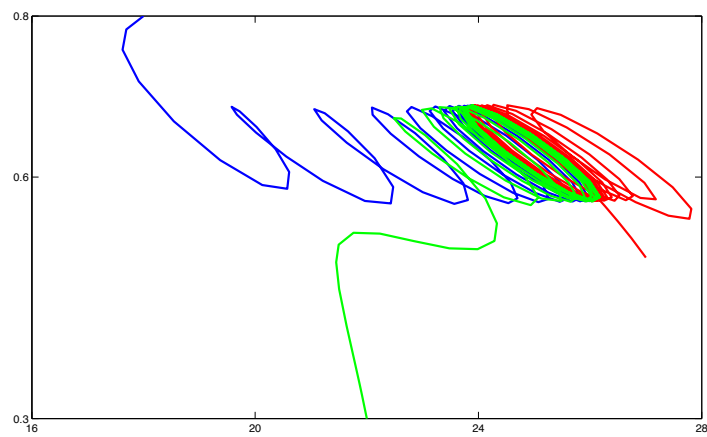


Fig. 3 Phase of predator-prey.

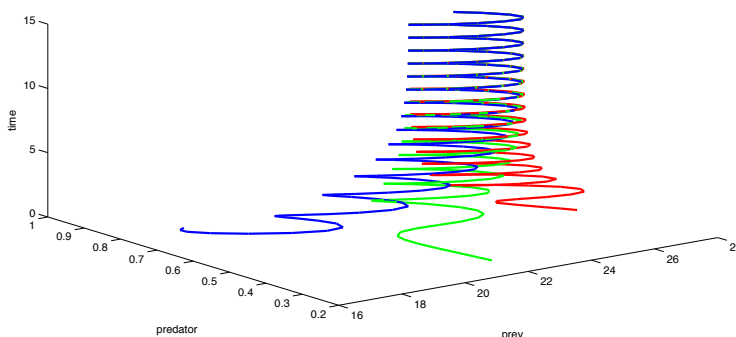


Fig. 4 Phase of predator-prey-time.

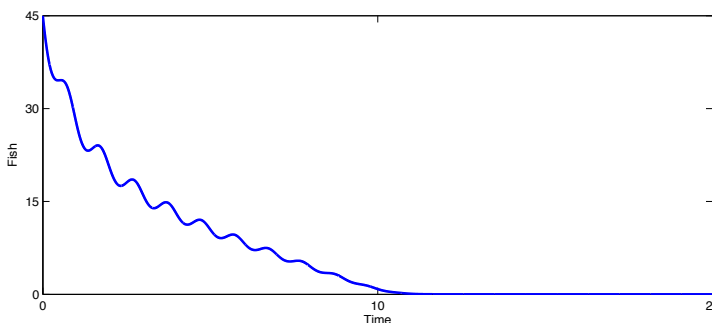


Fig. 5 Extinction of predator.

By a direct computation, One could easily verify that all conditions in Theorem 9 are satisfied, hence system (3) admits at least a positive 1-periodic solution. Figures 1 and 2 give variation of prey and predator densities respectively, Figure 3 corresponds to phase of predator-prey and Figure 4 the phase of predator-prey-time.

Example 2. Here, we state the case of extinction of predator. We consider system (3) with coefficients: $r(t) = 0.6 + 0.2\cos(2\pi t)$, $\tau(t) = 0.3$, $\gamma_G = 3$, $m_G = 0.3$, $m_B = 0.4$, $D = 5$, $e_B = 1$, $\gamma_B = 40$, and initial condition $G(\theta) = 30$, $B(\theta) = 45$ for all $\theta \in [-\tau^M, 0]$. For these values of parameters, hypothesis of Proposition 7 holds, then predator goes to extinction, see Figure 5.

5 Discussion

In this paper, a non-autonomous predator-prey model with time delay is investigated to show how fish populations may react to yearly water-level fluctuation in an artificial lake. By using comparison theorem, we prove the system is permanent under some appropriate conditions. If the system is periodic, some sufficient conditions are established, which guarantee the existence of a positive periodic solution of the system. Our results have showed that the permanence and the existence of positive periodic solution depend on the water-depth and on the delay. This study contributes to a better understanding of the effects of long-term water-level fluctuations on the fish population dynamics in Pareloup lake. A method based on the use of predation rate parameter $r(t)$ as indicator (which depends directly on the water level of the lake). The threshold between persistence and extinction depends critically on the predation rate $r(t)$. Indeed, we have shown that if the predation rate is not very high (i.e (H_1) , (H_2) hold), then both prey and predator species coexist. Ecologically speaking, if the acces-

sibility function $r(t)$ is between critical values, then the two species can coexist and tend to fluctuate with the same period as the environment. On the contrary, from proposition 7, at high levels of water, there are weak interactions between species and then the predator species goes to extinction. From the point of view of ecology, this phenomenon is not desirable. So, we also need to pay attention to the values of water level in order to keep sustainable developing of ecosystem.

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APPENDIX

Proof of lemma 4

Let $u(t) = r_2G(t) - \gamma_B(B(t) + D)$.

By condition (H_1) we have $u(0) < 0$. It is claimed that $u(t) < 0$ for all $t \geq 0$. if this not the case, there exists $t_0 > 0$ such that:

$$u(t_0) = 0 \quad \text{and} \quad \frac{du(t_0)}{dt} \geq 0.$$

The condition $u(t_0) = 0$ implies that

$$B(t_0) = \frac{r_2G(t_0)}{\gamma_B} - D.$$

From (3), we get

$$\frac{du}{dt}(t_0) = r_2 \frac{dG}{dt}(t_0) - \gamma_B \frac{dB}{dt}(t_0)$$

and

$$\begin{aligned} \frac{du}{dt}(t_0) = & -r_2 r(t_0) B(t_0) \frac{G(t_0)}{B(t_0) + D} - \gamma_B e_B r(t_0 - \tau(t_0)) B(t_0) \frac{G(t_0 - \tau(t_0))}{B(t_0 - \tau(t_0)) + D} \\ & + r_2 (\gamma_G + m_B) G(t_0) - \gamma_B m_B D - r_2 m_G G(t_0) G(t_0 - \tau(t_0)). \end{aligned}$$

Integrating the first and the second equation of (3) between the limits $t_0 - \tau(t_0)$ and t_0 ; we find

$$G(t_0) \leq G(t_0 - \tau(t_0)) e^{\gamma_G \tau^M}$$

and

$$B(t_0) \geq B(t_0 - \tau(t_0)) e^{-m_B \tau^M},$$

from which $G(t_0 - \tau(t_0)) \geq G(t_0) e^{-\gamma_G \tau^M}$ and $B(t_0 - \tau(t_0)) \leq B(t_0) e^{m_B \tau^M}$,
then

$$\begin{aligned} \frac{du}{dt}(t_0) \leq & -r_2 r(t_0) B(t_0) \frac{G(t_0)}{B(t_0) + D} - \gamma_B e_B r(t_0 - \tau(t_0)) B(t_0) \frac{G(t_0 - \tau(t_0))}{B(t_0 - \tau(t_0)) + D} \\ & + r_2 (\gamma_G + m_B) G(t_0) - \gamma_B m_B D - r_2 m_G e^{-\gamma_G \tau^M} (G(t_0))^2. \end{aligned}$$

It follows that

$$\frac{du}{dt}(t_0) \leq -r_2 m_G e^{-\gamma_G \tau^M} (G(t_0))^2 + r_2 (\gamma_G + m_B) G(t_0) - \gamma_B m_B D.$$

Condition (H_1) implies that $\frac{du}{dt}(t_0) < 0$ and we obtain a contradiction. This implies that $u(t) < 0$ for all $t \geq 0$.

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