PREDATOR–PREY DYNAMICS WITH SEASONAL WATER-LEVEL FLUCTUATIONS

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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. In this paper, we consider a seasonally varying predator–prey model to study the influence of water-level variations on the interaction between two species of fishes in an artificial lake. A seasonal variation of the water-level is introduced in the predation rate taking into account two values, leading to a general switched system. Permanence, stability and existence of an invariant domain containing at least one periodic solution are established. Our theoretical results confirm the assumption that the water exerts a strong influence on the interaction between fishes.

Keywords: Predator–Prey Model; Permanence; Stability; Periodic Solution.

1. Introduction and Mathematical Model

Environmental periodicity and fluctuations have great influence on the interaction between prey and predator fish. For example, in Refs. 1, 2 authors show that the random fluctuations play a crucial role in population dynamics, which can affect significantly the time behavior of predator–prey systems (see also Refs. 3, 4). The impact of water-level fluctuations on the species communities has been widely studied, with emphasis on the periodic forcing induced by seasonality.[5–11] Depending on the

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spatial and temporal extension, water-level fluctuations can influence the dynamics and structure of the prey as well as of the predator communities.[11] Recently, we developed a predator–prey model, given by a system of non-autonomous differential equations, to describe the impact of water-level in *Pareloup* lake on fish population dynamics.[6] The *Pareloup* lake, also known as Lac *de Salles-Curan*, is the largest lake in the *Midi-Pyrenees* region and the 5th largest lake in France (1,200 hectares). The water of the *Pareloup* lake is used by EDF, the French national electricity company, to generate electricity. 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.[7,11] Indeed, when the water-level is low, during the autumn, 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 Ref. 5 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 differential equations:

$$\begin{cases} \dfrac{dG}{dt} = G(\gamma_G - m_G G) - \min\left(r(t)\dfrac{G}{B+D}, \gamma_B\right)B, \\ \dfrac{dB}{dt} = e_B \min\left(r(t)\dfrac{G}{B+D}, \gamma_B\right)B - m_B B, \end{cases} \tag{1.1}$$

subject to positive initial conditions

$$G(0) = G_0 > 0, \quad B(0) = B_0 > 0, \tag{1.2}$$

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 the autumn, reflecting the high demand of electricity, γ_G and γ_B are the maximum consumption rate of resource by prey and predator, respectively. e_B is the conversion rate, m_G and m_B are the consumption rates of biomass by metabolism of prey and predator, respectively. D measures the other causes of mortality outside the metabolism and predation. The historical origin and applicability of this model are discussed in detail in Ref. 5. In their article, authors obtained sufficient conditions for the existence of a 1-periodic positive solution of system (1.1) by using the continuation theorem of coincidence degree theory.[12] More recently, Moussaoui *et al.*, in Ref. 13, investigated a more complex interaction among three species living in the *Pareloup* lake under seasonal succession. The authors have shown that the system is permanent under certain appropriate conditions and have obtained sufficient conditions to guarantee the existence of a 1-periodic positive solution. The existence of periodic solutions and their stability for a delayed version of (1.1) are studied in Ref. 14. In Ref. 15, 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. Through the proposed models, the obtained results confirm the assumption that the water-level fluctuations play a major role on the dynamic behavior of the predator–prey system.

In the present paper, unlike these works where the authors used a continuous 1-periodic predation rate function, we make the assumption that there are only two seasons each year. Therefore, we obtain a switched system modeling both situations with high and low level waters. The largest rate, corresponding to the low water-level arising during autumn and winter, while the smallest, corresponds to the high water-level arises during both spring and summer. Thus, we consider that periodicity occurs in the predation rates by switching between two levels as follows:

$$r(t) = \begin{cases} r_+ = r(1+\delta), & \text{High season,} \\ r_- = r(1-\delta), & \text{Low season,} \end{cases} \tag{1.3}$$

where r gives the mean predation rate, and $0 < \delta < 1$ represents the strength of the seasonal forcing.

Hence, a trajectory of system (1.1) is a concatenation of arcs of trajectories of the following systems:

$$\begin{cases} \dfrac{dG}{dt} = G(\gamma_G - m_G G) - \min\left(r_+ \dfrac{G(t)}{B+D}, \gamma_B\right) B, \\ \dfrac{dB}{dt} = e_B \min\left(r_+ \dfrac{G}{B+D}, \gamma_B\right) B - m_B B, \end{cases} \tag{1.4}$$

and

$$\begin{cases} \dfrac{dG}{dt} = G(\gamma_G - m_G G) - \min\left(r_- \dfrac{G}{B+D}, \gamma_B\right) B, \\ \dfrac{dB}{dt} = e_B \min\left(r_- \dfrac{G}{B+D}, \gamma_B\right) B - m_B B. \end{cases} \tag{1.5}$$

As a first step, we consider a model with $\delta = 0$, thus ignoring water-level variations. The resulting model is a system of ordinary differential equations, for which we study the persistence, the predator extinction and the stability of equilibria (Sec. 3). In the second model, we take into account the variations of water-level in the lake ($\delta \neq 0$), leading us to adapt the first model to this more realistic situation, for which the existence of an invariant domain, which contains all the annual periodic solutions of the switched system[a] is proved (Sec. 4). First of all, let us analyze the existence, the boundedness and the positivity of the solutions of the switched system (1.1)–(1.3) (Sec. 2).

2. Global Existence and Positivity of Solutions

In this section, we show that the switched model (1.1)–(1.3) is well-posed, in the sense that for any pair of positive initial conditions (G_0, B_0), (1.1)–(1.3) has a

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[a] We call switched system the system (1.1)–(1.2) with $r(t)$ given by (1.3).

unique solution which remains positive and bounded, and hence exists globally. To this end, we prove the following result.

Lemma 2.1. *Let* $h : \mathbb{R}^2 \to \mathbb{R}$ *be the function defined by,*

$$h : (x, y) \to \min(f(x, y), \gamma_B).$$

If f *is locally Lipschitz, then the function* h *is also locally Lipschitz.*

Proof. It is easy to see that

$$h(x, y) = \frac{1}{2}(f(x, y) + \gamma_B - |f(x, y) - \gamma_B|).$$

The form of h with respect to f obviously shows that if f is locally Lipschitz, then h is locally Lipschitz.

Hence, local existence and uniqueness of solutions of the switched system (1.1)–(1.3) are obtained for the corresponding Cauchy problem.[16,17] □

Regarding the positivity and boundedness of the solution for the system (1.1)–(1.3), we have the following proposition.

Proposition 2.1. (a) *The positive cone* $\mathbb{R}^2_+$ *is positively invariant for* (1.1)–(1.3).
(b) *All the solutions of the switched system* (1.1)–(1.3) *which initiate in* $\mathbb{R}^2_+$ *are ultimately bounded.*

Proof. See Appendix A. □

3. Prey–Predator Model in the Absence of Variations of Water-Level

In the absence of water-level variations ($\delta = 0$), we can assume that $r(t) = r$ for all $t \geq 0$. That is, the system takes the form

$$\begin{cases} \dfrac{dG}{dt} = G(\gamma_G - m_G G) - \min\left(r\dfrac{G}{B+D}, \gamma_B\right)B, \\ \dfrac{dB}{dt} = e_B \min\left(r\dfrac{G}{B+D}, \gamma_B\right)B - m_B B. \end{cases} \tag{3.1}$$

We make the following assumptions:

$$(H_0) : \gamma_G^2 > \frac{4m_G m_B D}{e_B},$$

$$(H_1) : r < \min\left(\frac{\gamma_B\,(B_0 + D)}{G_0}, \frac{4m_B m_G D\gamma_B}{(\gamma_G + m_B)^2}\right),$$

$$(H_2) : 0 < r_1 < r < r_2,$$

where $r_1 = \frac{\gamma_G - \sqrt{\gamma_G^2 - \frac{4m_G m_B D}{e_B}}}{2}$ and $r_2 = \frac{\gamma_G + \sqrt{\gamma_G^2 - \frac{4m_G m_B D}{e_B}}}{2}$.

3.1. *Persistence and permanence*

In this subsection, we analyze the persistence (weak and strong) and permanence behavior of system (3.1).

Definition 3.1 (Persistence). System (3.1) is said to be weakly persistent if every solution $(G(t), B(t))$ satisfies two conditions:

(i) $G(t) \geq 0, B(t) \geq 0, \ \forall\, t \geq 0$.
(ii) $\limsup_{t\to+\infty} G(t) > 0, \limsup_{t\to+\infty} B(t) > 0$.
System (3.1) is said to be strongly persistent if every solution $(G(t), B(t))$ satisfies the following condition along with the first condition of the weak persistence:
(iii) $\liminf_{t\to+\infty} G(t) > 0, \liminf_{t\to+\infty} B(t) > 0$.

Definition 3.2 (Permanence and non-permanence). System (3.1) is said to be permanent if there exist positive constants $0 < m \leq M$ such that,

$$\min\left\{\liminf_{t\to+\infty} G(t), \liminf_{t\to+\infty} B(t)\right\} \geq m,$$

$$\min\left\{\limsup_{t\to+\infty} G(t), \limsup_{t\to+\infty} B(t)\right\} \leq M,$$

for all solutions $(G(t), B(t))$ of system (1.1) with positive initial values.

System (1.1), whose solutions are bounded, is said to be non-permanent if there is a positive solution $(G(t), B(t))$ of (3.1) and such that,

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

Geometrically, persistence means that trajectories that initiate in a positive cone are eventually bounded away from coordinate planes. On the other hand, permanent coexistence (uniform persistence) implies the existence of a region in the phase space at a nonzero distance from boundary in which population vectors must lie ultimately. The last ensures the survival of species in biological sense.

To establish the persistence of system (3.1), we need to recall the following lemma, whose proof can be found in Ref. 18.

Lemma 3.1. *If* $a, b > 0$ *and* $\frac{dX}{dt} \leq$ *(respectively* $\geq$*)*$X(t)(a - bX(t))$, *with* $X(0) > 0$, *then we have*

$$\limsup_{t\to+\infty} X(t) \leq \frac{a}{b} \left(\textit{respectively} \liminf_{t\to+\infty} X(t) \geq \frac{a}{b}\right).$$

Our main result is stated in the following proposition.

Proposition 3.1. *Under hypotheses* $(H_1), (H_2)$, *then system* (3.1) *is permanent, that is, there exist positive constants* m_i, M_i $(i = 1, 2)$ *which are independent of the* *solution of system* (3.1), *such that for any positive solution* $(G(t), B(t))$ *of system* (3.1) *with the initial condition* $G_0 > 0,\ B_0 > 0$, *one has*

$$m_1 \leq \liminf_{t\to+\infty} G(t) \leq \limsup_{t\to+\infty} G(t) \leq M_1,$$

$$m_2 \leq \liminf_{t\to+\infty} B(t) \leq \limsup_{t\to+\infty} B(t) \leq M_2.$$

Proof. See Appendix B. □

In the next proposition, we are able to give sufficient conditions under which the given system is not persistent.

Proposition 3.2. *Let us denote by*

$$M_1 := \frac{\gamma_G}{m_G} \quad \textit{and} \quad M_2 := \frac{e_B r M_1}{m_B} - D. \tag{3.2}$$

If

$$(H_3): \ M_2 < 0,$$

that is, if $r < \frac{m_G m_B D}{e_B \gamma_G}$, *then the predator goes to extinction.*

Proof. See Appendix C. □

Remark 3.1. Biologically, it means that, when the predation rate is small enough, the predator disappears.

3.2. *Steady states analysis*

For dynamic population models in deterministic environments with constant parameters, it is meaningful to find the community equilibria where all the species have time independent values, that is, where all growth rates are zero. Classical two-species predator–prey models always possess at least three equilibrium points: (i) trivial equilibrium, (ii) axial equilibrium and (iii) positive interior equilibrium.[19]

As we mentioned in Appendix B, under hypothesis (H_1) system (3.1) is reduced to the simpler form

$$\begin{cases} \dfrac{dG}{dt} = G(\gamma_G - m_G G) - r\dfrac{GB}{B+D}, \\[2ex] \dfrac{dB}{dt} = e_B r \dfrac{GB}{B+D} - m_B B. \end{cases} \tag{3.3}$$

The equilibrium points for system (3.3) are given by (i) $E_0(0,0)$ (trivial equilibrium), (ii) $E_1(\frac{\gamma_G}{m_G}, 0)$ (predator-extinction equilibrium), and (iii) $E_*(G_*, B_*)$ (positive equilibrium), where

$$G_* = \frac{(\gamma_G - r) + \sqrt{(\gamma_G - r)^2 + \frac{4 m_G m_B D}{e_B}}}{2 m_G}, \quad B_* = \frac{e_B r G_*}{m_B} - D.$$

The existence of more interesting steady state E_*, where both prey and predator populations coexist, demands an extra condition,

$$(H_3^c) : r > \frac{m_G m_B D}{e_B \gamma_G}.$$

3.2.1. *Local stability*

It is straightforward, by simple algebraic computations, to see that (E_0) is always unstable, (E_1) is a stable node under (H_3) and a saddle under (H_3^c). Finally, the positive equilibrium (E_*) is locally stable whenever it exists, that is under (H_3^c).

3.2.2. *Global stability*

We have obtained the conditions for the existence of positive equilibrium and its local asymptotic stability. We have observed that instability of the boundary equilibrium E_1 gives support for the existence of positive interior equilibrium point E_*. The parametric condition for local asymptotic stability of E_* is given by (H_3^c). Now we analyze the global asymptotic stability of E_* by giving conditions under which the system (3.3) has no nontrivial periodic solutions. For this purpose we apply the Bendixson–Dulac divergence criterion for the stability of a periodic solution for planar systems.[17]

Let us construct the function $H(G,B) = \frac{1}{GB}$ such that $H(G,B) > 0$ for all $G > 0,\ B > 0$.

Using the notations

$$F_1(G,B) := G(t)\left(\gamma_G - m_G G(t)\right) - r\frac{G(t)B(t)}{B(t)+D}$$

and

$$F_2(G,B) := e_B r\frac{G(t)B(t)}{B(t)+D} - m_B B(t),$$

we get

$$\operatorname{div}(HF_1, HF_2) = \frac{\partial(HF_1)}{\partial G} + \frac{\partial(HF_2)}{\partial B} = -\frac{m_G}{B} - \frac{e_B r}{(B+D)^2} < 0.$$

This shows that $\operatorname{div}(HF_1, HF_2)$ does not change sign and is not identically zero in the positive quadrant of GB-plane. According to the Bendixson–Dulac criterion, it follows that the system (3.3) has no closed trajectory, and hence no periodic solution in the interior of the positive quadrant of GB-plane. Then $(G(t), B(t))$ tends either to $(\frac{\gamma_G}{m_B}, 0)$ or (G_*, B_*). We can state the following result.

Proposition 3.3. *System* (3.3) *cannot have any limit cycle in the interior of the positive quadrant.*

Therefore, results above in addition to the boundedness of the solutions prove the following result, which is simulated in Figs. 1 and 2.

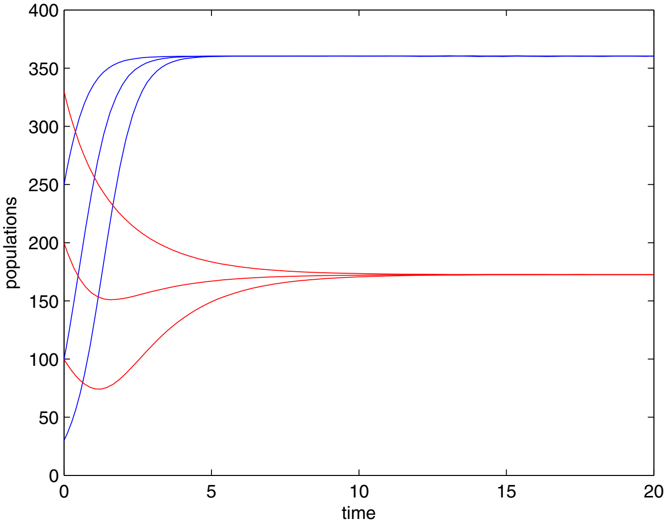

Fig. 1. Time series for stable solution. Blue curve represents prey population, red curve represents predator population, the fixed set of parameters are: $r = 0.8, m_G = 0.005, \gamma_G = 2.6, D = 0.4, e_B = 0.3$ and $m_B = 0.5$.

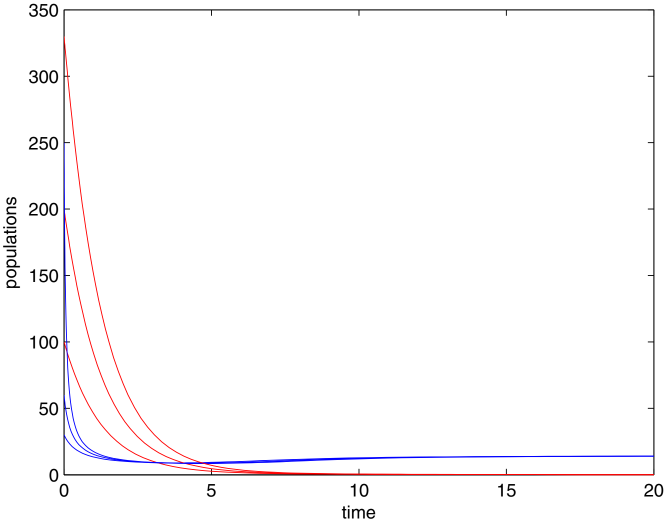

Fig. 2. Numerical solution of the system (3.1) with the set of parameters: $r = 0.5, m_G = 0.07, \gamma_G = 1, D = 2, e_B = 0.2, m_B = 0.8$ and $\gamma_B = 300$.

Corollary 3.1. (i) *If* $(H_1), (H_2)$ *and* (H_3^c) *hold, then the positive equilibrium* E_* *is globally asymptotically stable.*

(ii) *If* $(H_1), (H_2)$ *and* (H_3) *hold, then the positive equilibrium point* E_* *does not exist and the equilibrium* E_1 *is globally asymptotically stable.*

4. Piecewise Constant Model

The above discussion rests on the assumption that involved environmental parameters are all constants with respect to the time and to environmental fluctuations, for which we have dealt with analysis of the equilibria and we have derived the conditions for persistence of solutions. Now, in this section we are interested in analyzing the dynamical behavior of the system (1.1) with respect to the water-level in the lake ($\delta \neq 0$). As mentioned, the predation rate $r(t)$ depends on the season and predation peaks are higher in winter, reflecting the high demand of electricity, unlikely to the situation in summer season in which, due to the high level water, contacts are less frequent. A commonly used scheme takes $r(t)$ as a period one function (i.e., $r(t+1) = r(t)$ where t has units of years), see for example.[5,6,8] However, for the sake of the simplicity, we make the approximation (see Refs. 20, 21) that there are only two seasons each year as follows:

$$r(t) = \begin{cases} r_+ = r(1+\delta), & \text{High season}, \\ r_- = r(1-\delta), & \text{Low season}. \end{cases}$$

Over time the seasons change sequentially $High \to Low \to High \ldots$. The High season begins at times $t_n,\ n = 0, 2, 4, \ldots$, with a high predation rate r_+ and lasts for a time interval $\theta * t = T^-$ where t is the period length (i.e., a year) and $0 < \theta < 1$. This is followed by the Low season at times $t_n,\ n = 1, 3, 5, \ldots$, with low predation rate r_- and lasts for $(1-\theta) * t = T^+$. Hence, a trajectory of system (1.1) is a concatenation of arcs of trajectories of the following systems:

$$\begin{cases} \dfrac{dG}{dt}(t) = G(t)(\gamma_G - m_G G(t)) - \min\left(\dfrac{r_+ G(t)}{B(t)+D}, \gamma_B\right) B(t), \\ \dfrac{dB}{dt}(t) = e_B \min\left(\dfrac{r_+ G(t)}{B(t)+D}, \gamma_B\right) B(t) - m_B B(t), \end{cases} \tag{4.1}$$

and

$$\begin{cases} \dfrac{dG}{dt}(t) = G(t)(\gamma_G - m_G G(t)) - \min\left(\dfrac{r_- G(t)}{B(t)+D}, \gamma_B\right) B(t), \\ \dfrac{dB}{dt}(t) = e_B \min\left(\dfrac{r_- G(t)}{B(t)+D}, \gamma_B\right) B(t) - m_B B(t). \end{cases} \tag{4.2}$$

Throughout this section, we assume

$$(H_4) : \max\left(r_1, \frac{m_G m_B D}{e_B \gamma_G}\right) < r_- < r_+ < \min\left(r_2, \frac{\gamma_B (B_0 + D)}{G_0}, \frac{4 m_B m_G D \gamma_B}{(\gamma_G + m_B)^2}\right),$$

where r_1 and r_2 are defined in hypothesis (H_2) and are assumed to be positive.

Note that hypothesis (H_4) implies that all hypotheses (H_1), (H_2) and (H_3^c) are satisfied for each subsystem.

We shall prove the existence of periodic solution for system (1.1) by using Brouwer's Fixed Point Theorem.

First of all, let us rewrite systems (4.1) and (4.2) in a simpler form, as it has been done in the proof of Proposition 3.1, we can easily prove that for all $t \geq 0$,

$$r_+G(t) < \gamma_B(B(t)+D).$$

Thus, under assumption (H_4) we can reduce systems (4.1), (4.2) in the simpler forms

$$\begin{cases} \dfrac{dG}{dt}(t) = G(t)(\gamma_G - m_G G(t)) - \dfrac{r_+G(t)B(t)}{B(t)+D}, \\ \dfrac{dB}{dt}(t) = e_B\dfrac{r_+G(t)B(t)}{B(t)+D} - m_B B(t), \end{cases} \tag{4.3}$$

and

$$\begin{cases} \dfrac{dG}{dt}(t) = G(t)(\gamma_G - m_G G(t)) - \dfrac{r_-G(t)B(t)}{B(t)+D}, \\ \dfrac{dB}{dt}(t) = e_B\dfrac{r_-G(t)B(t)}{B(t)+D} - m_B B(t). \end{cases} \tag{4.4}$$

Since $r(t)$ is piecewise constant, the system (1.1) appears, in each interval of commutation, as an autonomous system. Straightforward calculations similar to the ones in the previous section show that the seasonal system (1.1) has in each interval, only one pseudo-steady state denoted $(G^*_\pm, B^*_\pm)$ which is globally asymptotically stable. Here we use the terminology pseudo-steady state for steady state of the system without periodicity (i.e., steady states of the sub-systems (4.3) and (4.4)). These two pseudo-steady states (G^*_+, B^*_+) and (G^*_-, B^*_-) are given by

$$G^*_+ = \frac{(\gamma_G - r_+) + \sqrt{(\gamma_G - r_+)^2 + \frac{4Dm_Gm_B}{e_B}}}{2m_G}, \quad B^*_+ = \frac{e_Br_+G^*_+}{m_B} - D,$$

$$G^*_- = \frac{(\gamma_G - r_-) + \sqrt{(\gamma_G - r_-)^2 + \frac{4Dm_Gm_B}{e_B}}}{2m_G}, \quad B^*_- = \frac{e_Br_-G^*_-}{m_B} - D.$$

Now we state our main results.

Theorem 4.1. *If the assumption* (H_4) *holds, there exists a compact, convex and positively invariant domain* S *for the system* (1.1)–(1.3) *and at least one annual periodic solution in* S.

Proof. See Appendix D. □

The periodic behavior of the solution of the switched model (1.1)–(1.3) is illustrated in Fig. 3, as can be observed the time horizon has been selected after the populations have reached a stable periodic behavior, which plays a similar role as a globally stable equilibrium does in the autonomous model.

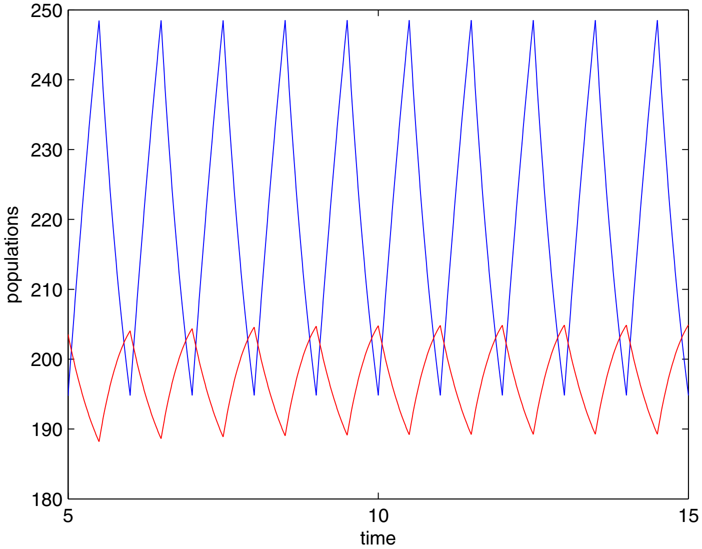

Fig. 3. Dynamic behavior of the switched system (1.1)–(1.3): Blue: $G(t)$, Red: $B(t)$, the parameters of the model are: $\gamma_G = 2.6, m_G = 0.005, m_B = 0.5, D = 0.4$ and $e_B = 0.3$.

5. Discussion

Aquatic ecosystems are often altered by human activities. This study provides preliminary results of the evolution of the ecosystems based on water management of the lake. We showed that variations in water-level of the lake are an important factor which is responsible for persistence or extinction in prey–predator relationships. Our first aim was to give a complete and rigorous analysis of existence of periodic solution of our system. In an ecological context, the existence of solutions should be viewed as a condition allowing for the survival of the species under consideration. The results of this study demonstrate that the dynamics of the system depends heavily on the fluctuation of the water-levels. The mathematical analysis presented in this work shows that, according to the variations of water-levels, one can make suitable predictions about the asymptotic behavior of the overall predator–prey system including the permanence, the periodicity, the global asymptotic stability and the extinction of species.

Because of ignoring the dependence of predation rate on water-levels, the autonomous model (model (3.1)) could not explain well how water-level variations can affect the distribution of fish species. Indeed, using stability theory of ordinary differential equations, it has been proved that the interior equilibrium exists under certain conditions and it is globally asymptotically stable. In the other hand, when we take into account the variation of water-levels (model (1.1)–(1.3)), we analytically proved under some conditions, the existence of an invariant domain

S containing at least one positive 1-periodic solution. These conditions depend on the switching predation rates r_+, r_- which depend directly on the water-levels of the lake. Ecologicaly speaking, if the water-levels are between critical values (condition (H_4)), then the two species can coexist and tend to fluctuate with the same period as the environment. On the contrary, from Proposition 3.2, at high levels of water, there are weak interactions between species and then the predator species goes to extinction. Also, using water volume as control, it is possible to keep the levels of the populations at a required state using the above control.

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Appendix A

Let the interval $[0, T_{\max})$ be the maximal interval of existence of a solution of the system (1.1)–(1.3).

(a) From system (1.1), it follows that $G = 0$ (respectively $B = 0$) is an invariant subset, that is, $G = 0$ (respectively $B = 0$) if and only if $G(t) = 0$ (respectively $B(t) = 0$) for some t. Thus if $G(0) > 0$ (respectively $B(0) > 0$), then $G(t) > 0$ (respectively $B(t) > 0$) for all $t \in [0, T_{\max})$.

(b) Let us consider $z(t) = e_B G(t) + B(t)$. Then

$$\frac{dz}{dt} + m_B z = e_B(\gamma_G + m_B)G - e_B m_G G^2 \leq \frac{e_B(\gamma_G + m_B)^2}{4m_G} = \eta.$$

We obtain

$$\begin{aligned} 0 < z(t) &\leq \frac{\eta}{m_B}(1 - e^{-m_B t}) + z(0)e^{-m_B t}. \\ &\leq \max\left\{z(0), \frac{\eta}{m_B}\right\} := \delta. \end{aligned} \tag{A.1}$$

From the well-known extension theorem,[16] we have $T_{\max} = +\infty$, therefore the solutions are bounded. Moreover, we have $\limsup_{t\to\infty} z(t) \leq \frac{\eta}{m_B}$, which is independent of the initial condition. Hence, all the solutions of (1.1)–(1.3) that initiate in $\mathbb{R}_+^2$ are confined in the region

$$\Omega = \left\{(G, B) \in \mathbb{R}_+^2 : e_B G(t) + B(t) \leq \frac{\eta}{m_B} + \varepsilon\right\},$$

for any $\varepsilon > 0$ as $t \to +\infty$.

Appendix B

First of all, using argument similar to the one displayed in Proposition 2 in Ref. 9, one can show that under (H_1), we have

$$rG(t) < \gamma_B(B(t) + D), \quad \text{for all } t \geq 0.$$

Consequently, under hypothesis (H_1) system (3.1) is reduced to the simpler form

$$\begin{cases} \dfrac{dG}{dt} = G(\gamma_G - m_G G) - r\dfrac{GB}{B+D}, \\ \dfrac{dB}{dt} = e_B r\dfrac{GB}{B+D} - m_B B. \end{cases} \tag{B.1}$$

To prove the (strong) persistence of system (3.1), we will use system (B.1) (which is equivalent to system (3.1) under hypothesis (H_1)).

As the variables G, B are positive, from the first equation of system (B.1), it follows that:

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

Using Lemma 3.1, we obtain

$$\limsup_{t\to+\infty} G(t) \leq \frac{\gamma_G}{m_G} := M_1. \tag{B.2}$$

Thus, for arbitrary $\varepsilon_1 > 0$, there exists a positive real number T_1 such that

$$G(t) \leq M_1 + \varepsilon_1, \quad \forall\, t \geq T_1.$$

Further, from the predator equation

$$\begin{aligned} \frac{dB}{dt} &\leq B\left(-m_B + \frac{e_B r(M_1 + \varepsilon_1)}{B+D}\right), \quad \forall\, t \geq T_1, \\ &= \frac{B}{B+D}(e_B r(M_1+\varepsilon_1) - m_B D - m_B B), \\ &\leq \frac{1}{D}B(e_B r(M_1+\varepsilon_1) - m_B D - m_B B). \end{aligned}$$

Using Lemma 3.1 and the arbitrariness of ε_1, we obtain

$$\limsup_{t\to+\infty} B(t) \leq \frac{e_B r M_1}{m_B} - D := M_2. \tag{B.3}$$

Thus, for arbitrary $\varepsilon_2 > 0$, there exists a positive real number $T_2 > T_1$ such that

$$B(t) \leq M_2 + \varepsilon_2, \quad \forall\, t \geq T_2.$$

Hence, system (3.1) is dissipative.

According to the first equation of system (B.1), it is easy to see that

$$\frac{dG}{dt} = G\left(\gamma_G - m_G G - \frac{rB}{B+D}\right) \geq G(\gamma_G - r - m_G G).$$

Using Lemma 3.1, we obtain

$$\liminf_{t\to\infty} G(t) \geq \frac{\gamma_G - r}{m_G} := m_1. \tag{B.4}$$

For arbitrary $\varepsilon_3 > 0$, there exists a positive real number T_3 such that

$$G(t) \geq m_1 - \varepsilon_3, \quad \forall\, t \geq T_3. \tag{B.5}$$

Thus, by applying (B.5) to the second equation of system (1.5), we obtain

$$\frac{dB}{dt} \geq \frac{B}{B+D}(e_B r(m_1 - \varepsilon_3) - m_B D - m_B B),$$

and for $t \geq T_4 = \max\{T_2, T_3\}$, we get

$$\frac{dB}{dt} \geq \frac{1}{M_2 + \epsilon_2 + D} B(e_B r(m_1 - \epsilon_3) - m_B D - m_B B), \quad \forall\, t \geq T_4.$$

Using Lemma 3.1 and the arbitrariness of ε_2 and ε_3, we obtain

$$\liminf_{t\to+\infty} B(t) \geq \frac{e_B r m_1}{m_B} - D := m_2. \tag{B.6}$$

Note that m_2 is positive, indeed,

$$m_2 = \frac{e_B r(\gamma_G - r)}{m_G m_B} - D = \frac{-e_B r^2 + e_B \gamma_G r - m_G m_B D}{m_G m_B}.$$

Hence, the numerator has two zeros given by r_1 and r_2, which are defined in (H_2). If hypothesis (H_2) holds, then the numerator is strictly positive and then m_2 and M_2 are also strictly positive.

Inequalities (B.2), (B.3), (B.4) and (B.6) show that under the assumptions of the Proposition 3.1, system (3.1) is permanent.

Appendix C

Using the upper bounds for G, from the predator equation, we have

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

then

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

Thus, under the given hypothesis, $B(t) \to 0$ as $t \to +\infty$. That is, the predator population goes to extinction.

Appendix D

The population dynamics are governed by the system (1.1)–(1.3). Similarly to Proposition 3.1, one can easily prove that under hypothesis (H_4), the system (1.1)–(1.3) is permanent, that is, any positive solution $(G(t), B(t))$ of system (1.1)–(1.3) satisfies:

$$0 < m_1^+ \le \liminf_{t\to+\infty} G(t) \le \limsup_{t\to+\infty} G(t) \le M_1,$$

$$0 < m_2^- \le \liminf_{t\to+\infty} B(t) \le \limsup_{t\to+\infty} B(t) \le M_2^+,$$

where

$$m_1^+ = \frac{\gamma_G - r_+}{m_G}, \quad m_2^- = \frac{e_B r_- m_1^+}{m_B} - D,$$

$$M_1 = \frac{\gamma_G}{m_G}, \quad M_2^+ = \frac{e_B r_+ M_1}{m_B} - D.$$

We define

$$S = \{(G,B) \in \mathbb{R}^2 \,|\, 0 < m_1^+ \le G(t) \le M_1, m_2^- \le B(t) \le M_2^+\}.$$

By a standard comparison argument, one can easily show that S is positively invariant with respect to system (1.1)–(1.3).

Define a shift operator, which is also known as a Poincaré mapping $T_k : \mathbb{R}_+^2 \to \mathbb{R}_+^2$ as follows:

$$T_k(Z_0) = Z(k, Z_0),$$

where $k \in \mathbb{N}^*$ and $Z(t, Z_0)$ is the solution of 1-periodic system (1.1) starting from point (G_0, B_0) at time $t = 0$.

According to discussion above, the set S is positively invariant with respect to system (1.1)–(1.3) and hence, operator T_k defined above maps S into itself, i.e., $T_k(S) \subset S$. Since the solution of (1.1)–(1.3), is continuous with respect to the initial value, the operator T_k is continuous. It is not difficult to show that S is a bounded, closed, convex set in $\mathbb{R}^2$. Hence, using Brouwer's Fixed Point Theorem, T_k has at least one fixed point in S. That is to say, under condition (H_4), the system (1.1)–(1.3) has at least one positive 1-periodic solution. This completes the proof.