

R_0 and sensitivity analysis of a predator-prey model with seasonality and maturation delay

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ABSTRACT

Coexistence and seasonal fluctuations of predator and prey populations are common and well documented in ecology. Under what conditions can predators coexist with prey in a seasonally changing environment? What factors drive long-term population cycles of some predator and prey species? To answer these questions, we investigate an improved predator-prey model based on the Rosenzweig–MacArthur [1] model. Our model incorporates seasonality and a predator maturation delay, leading to a system of periodic differential equations with a time delay. We define the basic reproduction ratio R_0 and show that it is a threshold parameter determining whether the predators can coexist with the prey. We show that if $R_0 < 1$, then the prey population has seasonal variations and the predator population goes extinct. If $R_0 > 1$, then the prey and the predators coexist and fluctuate seasonally. As an example, we study a *Daphnia*-algae system and explore possible mechanisms for seasonal population cycles. Our numerical simulations indicate that seasonal *Daphnia*-algae cycles are attributed to seasonality rather than *Daphnia* maturation delay or *Daphnia*-algae interaction. The *Daphnia* maturation delay, the amplitude of algae growth rate and the amplitude of the carrying capacity are found to affect the amplitude of cycles and average population levels. Our sensitivity analysis shows that R_0 is most sensitive to *Daphnia* death rate.

1. Introduction

The phenomena of coexistence and seasonal oscillations in predator and prey populations are ubiquitous in nature. For instance, monthly sampling from 2004 to 2008 shows that planktons, macrozoobenthos, shrimps and fish populations in the Gironde estuary exhibit marked seasonal variations [2]. Estuarine areas provide these species with habitats for reproduction, nursery, feeding, residence and migration [3], and provide human societies with valuable resources and services [4]. Human activities such as fishing, pumping and harbouring have increasing negative effects on water quality, and better managements are urgently needed to protect estuaries. To design effective protection measures, an improved understanding of the population dynamics of biological species under the effect of seasonal variations is essential. Understanding of seasonal fluctuations of prey and predator species is also important for biocontrol of some pest populations. In Benin, West Africa, a natural enemy *Typhlodromalus aripo* were introduced to control the pest mite *Mononychellus tanajoa* population, and studies found that the period of the pest-enemy fluctuations coincide with the rainfall pattern and start of dry season annually [5]. Ecologists are monitoring the long-term dynamics of the ecosystem, in an effort to identify key

factors that promote the persistence of predators so that the pest population can be effectively controlled [6].

Many seasonal factors such as temperature, sunlight, rainfall, humidity, wind and salinity can impact the dynamics of predator-prey systems. Mathematical models have been proposed to study long-term dynamics of predator-prey systems subject to seasonal changes (see, e.g., [7–10] and the references therein). Many epidemic models of infectious diseases that include seasonality have also been studied (see, e.g., [11–13] and the references therein). In epidemiology, the basic reproduction number R_0 is defined as the number of new infections produced by a typical infectious agent during its infectious period in a totally susceptible community. It is known that R_0 is a threshold parameter in the sense that the disease can be eliminated if $R_0 < 1$ and will persist if $R_0 > 1$ (see, e.g., [14–17]). In ecology, a similar threshold parameter has also been used to study biological invasion or coexistence of predator and prey populations. However, there are quite a few papers that employ the approach from epidemiology to define the threshold parameter for ecological models (see [18] and the references therein). Recently, Zhao [19] established the theory of basic reproduction ratio R_0 for periodic and time-delayed compartmental epidemic models. We will use the method in [19] to define R_0 and then

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explore whether R_0 is the threshold parameter that determines persistence or extinction of predators in the presence of prey under a seasonally changing environment. It is of great interest to see how R_0 depends on seasonal factors and how R_0 is sensitive to each parameter.

In addition to the conditions for coexistence, mechanisms that induce population cycles have also been studied in the literature. Since the pioneering work on Lotka-Volterra predator-prey model [20,21] and Rosenzweig–MacArthur model [1], various models have been proposed to explore the mechanisms behind the observed population cycles. Turchin and Batzli [22] revealed that the driver of oscillations was the interplay between lemmings and food supply. Hanski et al. [23] attributed the reason for cycles to the interaction between lemmings and their predators. Wang and Kuang [10] found that neither seasonal factors nor the lemming mortality rate and the moss growth rate could result in multi-year cycles. Some recent works highlighted the potential roles of predator maturation delay in causing multi-year population cycles among small mammals. May [24,25] concluded that time delay was correlated with cycle period and cycle amplitude by studying general predator-prey models. Gourley and Kuang [26] showed that predator maturation delays can generate population cycles. Wang et al. [27] constructed a series of predator-prey models with time delays to investigate multi-year population cycles including a 4-year lemming cycle, a 10-year snowshoe hare cycle and a 38-year moose cycle. They showed that the cycle period was almost completely determined by the predator maturation delay, whereas its amplitude was greatly affected by the functional response. In our study, we investigate if the predator maturation delay can be the causal mechanism of other predator-prey population cycles such as zooplankton-phytoplankton and fish-zooplankton.

In this paper, we develop a general predator-prey interaction model which takes into account seasonality and predator maturation delay. Mathematically, the model is a periodic system of delay differential equations. We derive the basic reproduction ratio R_0 and prove that R_0 is a threshold parameter determining whether the predators coexist and fluctuate seasonally with the prey. We also use the interaction of *Daphnia* and algae as an example to investigate the roles of seasonality and predator maturation delay in determining population cycles.

The paper is organized as follows. In the next section, we present the model. In Section 3, we establish the threshold dynamics of the model in terms of the basic reproduction ratio. In Section 4, we carry out numerical simulations for the *Daphnia*-algae interaction. In Section 5, we discuss our results and their biological implications, and propose some future research directions.

2. Model formulation

The Rosenzweig–MacArthur model [1] is one of the most frequently used predator-prey models in the literature and it is given by the following system:

$$\begin{aligned} \frac{dB(t)}{dt} &= rB(t)\left(1 - \frac{B(t)}{K}\right) - \gamma \frac{B(t)}{K_1 + B(t)}P(t), \\ \frac{dP(t)}{dt} &= \beta\gamma \frac{B(t)}{K_1 + B(t)}P(t) - \delta P(t). \end{aligned} \tag{1}$$

Here $B(t)$ and $P(t)$ are the densities of prey and predator populations at time t , respectively. We assume that the prey population grows according to the logistic law with the maximum per capita prey growth rate r and the carrying capacity K . The functional response is of Holling type II, with the per capita predation rate γ and the half-saturation predation constant K_1 . The parameter β is the conversion rate of prey biomass to predator biomass. The death rate of predators is δ .

Wrzosek [28] showed that the Rosenzweig–MacArthur model admits a unique and globally stable attractor which is either a limit cycle or an equilibrium. Gourley and Kuang [26] and Li et al. [29] improved the Rosenzweig–MacArthur model by incorporating a constant predator maturation delay and a general functional response with Holling type II

being a special case. Gourley and Kuang showed that, if the death rate of immature predators is nonzero, then the system has a globally attractive equilibrium for small and large values of predator maturation delays. Their linear stability analysis showed that sustainable oscillations can be generated by a window of values in the predator maturation delay if the resource is dynamic [26]. Li et al. [29] demonstrated that stability switches by varying the time delay are accompanied by bounded global Hopf branches. They also showed that multiple Hopf branches are nested when they exist and that coexistence of two or more stable limit cycles can be produced by the overlap. Feng et al. [30] extended the Rosenzweig–MacArthur model to an intraguild predation model in which both the predator and the prey can be consumed by the super-predator. They investigated the stability of the coexistence equilibrium. Banerjee and Volpert [31] developed a Rosenzweig–MacArthur type reaction-diffusion predator-prey model with non-local resource consumption. They constructed global *bifurcation* diagrams to describe the pattern transitions.

We develop our model by considering predator maturation delay and seasonality in the Rosenzweig–MacArthur model (1). We assume that the time delay associated with predator maturation is τ , and that the death rates for matured and immature predators are given by functions $\delta(t)$ and $\delta_j(t)$, respectively. Thus, the probability that predators survive the maturation period is given by the exponential term $e^{-\int_{t-\tau}^t \delta_j(s) ds}$. We assume that the conversion rate β and the delay τ are positive constants. We incorporate seasonality in our model by assuming that all the other parameters $r(t)$, $K(t)$, $\gamma(t)$, $K_1(t)$, $\delta(t)$ and $\delta_j(t)$ are positive, continuous and ω -periodic functions. This leads to the following model system:

$$\begin{aligned} \frac{dB(t)}{dt} &= r(t)B(t)\left(1 - \frac{B(t)}{K(t)}\right) - \gamma(t) \frac{B(t)}{K_1(t) + B(t)}P(t), \\ \frac{dP(t)}{dt} &= \beta\gamma(t - \tau)e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{B(t - \tau)}{K_1(t - \tau) + B(t - \tau)}P(t - \tau) \\ &\quad - \delta(t)P(t). \end{aligned} \tag{2}$$

It can be verified that function $e^{-\int_{t-\tau}^t \delta_j(s) ds}$ is also ω -periodic. Thus, model (2) is an ω -periodic system of functional differential equations. The biological interpretations for all the variables and parameters are given in Table 1.

3. Threshold dynamics

In this section, we study the dynamics of system (2). Let $C = C([- \tau, 0], \mathbb{R}^2)$, $C^+ = C([- \tau, 0], \mathbb{R}_+^2)$. Then C is an ordered Banach space equipped with the maximum norm and the positive cone C^+ . For any given continuous function $v: [- \tau, \sigma] \rightarrow \mathbb{R}^2$ with $\sigma > 0$, we define $v_t \in C$ by

$$v_t(\theta) = (v_1(t + \theta), v_2(t + \theta)), \quad \forall \theta \in [- \tau, 0],$$

for any $t \in [0, \sigma]$.

Lemma 1. For any $\varphi \in C^+$, system (2) has a unique nonnegative solution through φ , and solutions are ultimately bounded.

Table 1
Biological interpretations for variables and parameters of model (2).

Variable and Parameter	Description
$B(t)$	Prey population density
$P(t)$	Predator population density
$r(t)$	Maximal per capita growth rate of prey
$K(t)$	Prey carrying capacity
$\gamma(t)$	Maximal per capita predation rate
$K_1(t)$	Half-saturation constant of predators' functional response
β	Conversion rate of prey to predator
τ	Predator maturation delay
$\delta(t)$	Matured predator death rate
$\delta_j(t)$	Immatured predator death rate

Linearizing system (2) at the predator-free solution $(x^*(t), 0)$, we obtain a linear equation for the predator population:

$$\frac{dP(t)}{dt} = \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)x^*(t-\tau)}{K_1(t-\tau) + x^*(t-\tau)} P(t-\tau) - \delta(t)P(t). \tag{3}$$

Define a map $F: \mathbb{R} \rightarrow \mathcal{L}(C([- \tau, 0], \mathbb{R}))$ and a continuous function $V(t)$ by

$$F(t)\psi = \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)x^*(t-\tau)}{K_1(t-\tau) + x^*(t-\tau)} \psi(-\tau), \quad V(t) = \delta(t).$$

Then the internal evolution of the predator population is given by the equation:

$$\frac{dv(t)}{dt} = -V(t)v(t).$$

Let $\Phi(t, s)$, $t \geq s$, be the evolution operator of the above linear system. That is, $\Phi(t, s)$ satisfies

$$\frac{\partial}{\partial t} \Phi(t, s) = -V(t)\Phi(t, s), \quad \forall t \geq s,$$

and

$$\Phi(s, s) = 1, \quad \forall s \in \mathbb{R}.$$

It then easily follows that

$$\Phi(t, s) = e^{-\int_s^t V(r) dr} = e^{-\int_s^t \delta_j(r) dr}.$$

Let C_ω be the ordered Banach space of all continuous and ω -periodic functions from \mathbb{R} to \mathbb{R} , equipped with the maximum norm, and its positive cone $C_\omega^+ := \{v \in C_\omega : v(t) \geq 0 \text{ for all } t \in \mathbb{R}\}$.

Suppose that $v \in C_\omega$ is the initial distribution of mature predators. Then for any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly matured predators at time $t-s$, which are produced by the predators who were introduced over the time interval $[t-s-\tau, t-s]$. Then $\Phi(t, t-s)F(t-s)v_{t-s}$ is the distribution of those predators who newly matured at time $t-s$ and remain alive at time t . It follows that

$$\int_0^\infty \Phi(t, t-s)F(t-s)v_{t-s}(\cdot) ds = \int_0^\infty \Phi(t, t-s)F(t-s)v(t-s+\cdot) ds$$

is the distribution of cumulative new mature predators at time t produced by all those mature predators introduced at a time previous to t .

Define a linear operator $L: C_\omega \rightarrow C_\omega$ by

$$[Lv](t) = \int_0^\infty \Phi(t, t-s)F(t-s)v(t-s+\cdot) ds, \quad \forall t \in \mathbb{R}, \quad v \in C_\omega.$$

Following [19], we define $R_0 = \rho(L)$, the spectral radius of L . The solution map $S(t)$ of system (3) is defined by $S(t)\varphi = u_t(\varphi)$, $t \geq 0$, where $u_t(\varphi) = u(t, \varphi)$ is the unique solution of (3) with $u_0 = \varphi \in C([- \tau, 0], \mathbb{R})$. Then $S := S(\omega)$ is the Poincaré map associated with linear system (3). Let $\rho(S)$ be the spectral radius of S . By Theorem 2.1 of [19], we have the following result.

Lemma 2. $R_0 - 1$ has the same sign as $\rho(S) - 1$.

Let

$$X = C([- \tau, 0], \mathbb{R}_+^2) \quad \text{and} \quad X_0 = \{\phi = (\phi_1, \phi_2) \in X : \phi_2(0) > 0\}.$$

Theorem 1. The following statements hold:

- (i) If $R_0 < 1$, then the predator-free periodic solution $(x^*(t), 0)$ is globally attractive for system (2) in $X \setminus \{(0, 0)\}$;
- (ii) If $R_0 > 1$, then system (2) admits a positive ω -periodic solution, and there exists $\eta > 0$ such that any solution $(B(t, \varphi), P(t, \varphi))$ of system (2) with $\varphi \in X_0$ satisfies

$$\liminf_{t \rightarrow \infty} (B(t, \varphi), P(t, \varphi)) \geq (\eta, \eta).$$

Proof. Since $\beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)x^*(t-\tau)}{K_1(t-\tau) + x^*(t-\tau)} > 0$, it follows from Theorem 3.6.1 of [32] and Lemma 5.3.2 of [33] that, for each $t \geq 2\tau$, linear operator $S(t)$ is compact and strongly positive on $C([- \tau, 0], \mathbb{R})$. Choose an integer $n_0 > 0$ such that $n_0\omega \geq 2\tau$. Since $S^{n_0} = S(n_0\omega)$, Lemma 3.1 of [34] implies that $\rho(S)$ is a simple eigenvalue of S with a strongly positive eigenvector, and the modulus of any other eigenvalue is less than $\rho(S)$. Let $\mu = \frac{\ln \rho(S)}{\omega}$. Using the same proof of Proposition 2.1 of [35], we can show that there is a positive ω -periodic function $v(t)$ such that $u(t) = e^{\mu t}v(t)$ is a positive solution of system (4).

In the case $R_0 < 1$, we have $\rho(S) < 1$. Let $S_\epsilon := S_\epsilon(\omega)$ be the Poincaré map associated with the following perturbed linear ω -periodic system:

$$\frac{dP(t)}{dt} = \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)(x^*(t-\tau) + \epsilon)}{K_1(t-\tau) + (x^*(t-\tau) + \epsilon)} P(t-\tau) - \delta(t)P(t). \tag{4}$$

Since $\lim_{\epsilon \rightarrow 0} \rho(S_\epsilon) = \rho(S) < 1$, for sufficiently small $\epsilon > 0$ we have $\rho(S_\epsilon) < 1$. As discussed above, there exists $\epsilon > 0$ and a positive ω -periodic function $v_\epsilon(t)$ such that $u_\epsilon(t) = e^{\mu_\epsilon t}v_\epsilon(t)$ is a positive solution of system (4), where $\mu_\epsilon = \frac{\ln \rho(S_\epsilon)}{\omega} < 0$. Clearly, $\lim_{t \rightarrow \infty} u_\epsilon(t) = 0$.

For any given $\phi \in X \setminus \{(0, 0)\}$, let $u(t, \phi) = (B(t), P(t))$. From the proof of Lemma 1, there exists a sufficiently large integer $n_1 > 0$ such that $n_1\omega \geq \tau$ and $B(t) < x^*(t) + \epsilon$ for all $t \geq n_1\omega - \tau$. We then have

$$\frac{dP(t)}{dt} \leq \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)(x^*(t-\tau) + \epsilon)}{K_1(t-\tau) + (x^*(t-\tau) + \epsilon)} P(t-\tau) - \delta(t)P(t)$$

for all $t \geq n_1\omega$. Choose a sufficiently large number $N > 0$ such that $P(t) \leq Nu_\epsilon(t)$ for all $t \in [n_1\omega - \tau, n_1\omega]$. Then the comparison theorem for delay differential equations ([33, Theorem 5.1.1]) implies that $P(t) \leq Nu_\epsilon(t)$ for all $t \geq n_1\omega$. Hence, $\lim_{t \rightarrow \infty} P(t) = 0$. Using the chain transitive sets arguments (see Theorem 3.6 of [13]), it follows that $\lim_{t \rightarrow \infty} (B(t) - x^*(t)) = 0$. This proves statement (i).

In the case $R_0 > 1$, we have $\rho(S) > 1$. Let $\partial X_0 := X \setminus X_0 = \{\phi \in X : \phi_2(0) = 0\}$. Let $Q(t)$ be the solution map of system (2) on X defined by $Q(t)\varphi = u_t(\varphi)$, $t \geq 0$, where $u_t(\varphi) = u(t, \varphi)$ is the unique solution of system (2) satisfying $u_0 = \varphi \in X$. Then $Q := Q(\omega)$ is the Poincaré map associated with system (2). It is easy to see that $Q(t)X_0 \subseteq X_0$ for all $t \geq 0$. Lemma 1 implies that the discrete-time system $\{Q^n: X \rightarrow X\}_{n \geq 0}$ is point dissipative and Q^n is compact for sufficiently large n (see [32, Theorem 3.6.1]). It then follows from [36, Theorem 2.9] that Q admits a global attractor in X .

Let $M_1 = (0, 0)$, $M_2 = (x_0^*, 0)$, where $x_0^*(\theta) = x^*(\theta)$ for all $\theta \in [-\tau, 0]$. Since $\lim_{\phi \rightarrow M_1} (Q(t)\phi - M_1) = 0$ uniformly for $t \in [0, \omega]$, for any given $\delta_0 > 0$, there exists $\delta_1 > 0$ such that for any $\phi \in X_0$ with $\|\phi - M_1\| < \delta_1$, we have $\|Q(t)\phi - M_1\| < \delta_0$ for all $t \in [0, \omega]$.

Claim 1. $\limsup_{n \rightarrow \infty} \|Q(n\omega)\phi - M_1\| \geq \delta_1$ for all $\phi \in X_0$.

Suppose that $\limsup_{n \rightarrow \infty} \|Q(n\omega)\psi - M_1\| < \delta_1$ for some $\psi \in X_0$. Then there exists $N_1 > 0$ such that $\|Q(n\omega)\psi - M_1\| < \delta_1$ for all $n \geq N_1$. For $t \geq N_1\omega$, we have $t = t' + n\omega$, with $n \geq N_1$ and $t' \in [0, \omega]$, and hence, $\|Q(t)\psi - M_1\| = \|Q(t')Q(n\omega)\psi - M_1\| < \delta_0$. It follows that $B(t, \psi) < \delta_0$ and $P(t, \psi) < \delta_0$ for all $t \geq N_1\omega$. Since $\psi \in X_0$ and $Q(t)X_0 \subseteq X_0$, we have $P(t, \psi) > 0$ for all $t > 0$. Let $\delta_0 = \min_{t \in [N_1\omega, (N_1+1)\omega]} P(t, \psi)$, then $P(t, \psi) \geq \delta_0$ for $t \in [N_1\omega, (N_1+1)\omega]$, which contradicts the fact that $P(t, \psi) < \delta_0$ for all $t \geq N_1\omega$. This proves Claim 1.

Since $\lim_{\phi \rightarrow M_2} \|Q(t)\phi - Q(t)M_2\| = 0$ uniformly for $t \in [0, \omega]$, given $\epsilon > 0$, there exists $\eta_1 > 0$ such that, for $\phi \in X_0$ with $\|\phi - M_2\| < \eta_1$, we have $\|Q(t)\phi - Q(t)M_2\| < \epsilon$ for all $t \in [0, \omega]$.

Claim 2. $\limsup_{n \rightarrow \infty} \|Q(n\omega)\phi - M_2\| \geq \eta_1$ for all $\phi \in X_0$.

Suppose that $\limsup_{n \rightarrow \infty} \|Q(n\omega)\psi - M_2\| < \eta_1$ for some $\psi \in X_0$. Then there exists $N_2 > 0$ such that $\|Q(n\omega)\psi - M_2\| < \eta_1$ for all $n \geq N_2$. For any $t \geq N_2\omega$, we have $t = t' + n\omega$ with $n \geq N_2$, $t' \in [0, \omega]$, and hence, $\|Q(t)\psi - Q(t)M_2\| = \|Q(t')Q(n\omega)\psi - Q(t')Q(n\omega)M_2\| = \|Q(t')Q(n\omega)\psi - Q(t')Q(n\omega)M_2\| = \|Q(t')Q(n\omega)\psi - Q(t')M_2\| < \epsilon$

$t \geq N_2\omega$. Therefore, $B(t-\tau) > x^*(t-\tau) - \epsilon$ for all $t \geq N_2\omega + \tau$. Let ρ_ϵ

be the spectral radius of the Poincaré map associated with the following system:

$$\frac{dy(t)}{dt} = \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)(x^*(t-\tau) - \epsilon)}{K_1(t-\tau) + (x^*(t-\tau) - \epsilon)} y(t-\tau) - \delta(t)y(t). \tag{5}$$

Then $\lim_{\epsilon \rightarrow 0^+} \rho_\epsilon = \rho(S) > 1$. Fix a sufficiently small ϵ such that $\rho_\epsilon > 1$ and $x^*(t-\tau) - \epsilon > 0$. By similar arguments as those in the case $R_0 < 1$, system (5) has a solution $w_\epsilon(t) = e^{\lambda_\epsilon t} z_\epsilon(t)$, where $z_\epsilon(t)$ is positive and ω -periodic, $\lambda_\epsilon = \frac{\ln \rho_\epsilon}{\omega} > 0$. Clearly, $\lim_{t \rightarrow \infty} w_\epsilon(t) = \infty$. For $t \geq N_2\omega + \tau$, we have

$$\begin{aligned} \frac{dP(t)}{dt} &= \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)B(t-\tau)}{K_1(t-\tau) + B(t-\tau)} P(t-\tau) - \delta(t)P(t) \\ &> \beta e^{-\int_{t-\tau}^t \delta_j(s) ds} \frac{\gamma(t-\tau)(x^*(t-\tau) - \epsilon)}{K_1(t-\tau) + (x^*(t-\tau) - \epsilon)} P(t-\tau) - \delta(t)P(t). \end{aligned}$$

Since $Q(t)X_0 \subseteq X_0$ for $t \geq 0$, we have $P(t, \phi) > 0$ for $t \geq 0$. Then we can choose a sufficiently small $k > 0$ such that

$$P(t, \phi) \geq kw_\epsilon(t) \quad \text{for all } t \in [N_2\omega + \tau, N_2\omega + 2\tau].$$

By Theorem 5.1.1 of [33], it follows that

$$P(t, \phi) \geq kw_\epsilon(t) \quad \text{for all } t \geq N_2\omega + 2\tau.$$

Hence, $\lim_{t \rightarrow \infty} P(t, \phi) = \infty$, which contradicts the ultimate boundedness of the solution. This proves Claim 2.

Define $M_\partial := \{\phi \in \partial X_0: Q(t)(\phi) \in \partial X_0, \forall t \geq 0\}$. For any given $\phi \in M_\partial$, we have $P(t, \phi) = 0$ for all $t \geq 0$. From the first equation of system (2), it is easy to see that if $\phi_1(0) = 0$, then $\lim_{t \rightarrow \infty} B(t, \phi) = 0$; if $\phi_1(0) > 0$, then $\lim_{t \rightarrow \infty} (B(t, \phi) - x^*(t)) = 0$. Thus, $\bigcup_{\phi \in M_\partial} \omega(\phi) \subseteq \{M_1, M_2\}$ and no subset of $\{M_1, M_2\}$ forms a cycle in ∂X_0 . With the above two claims, we see that M_1 and M_2 are isolated invariant sets for Q in X , and $W^s(M_i) \cap X_0 = \emptyset$, $i = 1, 2$, where $W^s(M_i)$ is the stable set of M_i for Q , $i = 1, 2$. By the acyclicity theorem on uniform persistence for maps (see Theorem 1.3.1 and Remark 1.3.1 of [37]), it follows that $Q: X \rightarrow X$ is uniformly persistent with respect to X_0 .

Note that there exists an equivalent norm for $C([-\tau, 0], \mathbb{R}^2)$ such that for each $t > 0$, the solution map $Q(t)$ of system (2) is a κ -contraction on $C([-\tau, 0], \mathbb{R}_+^2)$, where κ is the Kuratowski measure of non compactness (see Theorem 3.6.1 of [32]). It then follows from Theorem 4.5 of [36] that system (2) admits an ω -periodic solution $Q(t)\phi^*$ with $\phi^* \in X_0$. Then $B(t, \phi^*) \geq 0$, $P(t, \phi^*) > 0$ for all $t \geq 0$. We claim that there exists some $\bar{t} \in [0, \omega]$ such that $B(\bar{t}, \phi^*) > 0$. Assuming otherwise, then $B(t, \phi^*) \equiv 0$ for all $t \geq 0$, due to the periodicity of $B(t, \phi^*)$. From the second equation of system (2), we get

$$\frac{dP(t, \phi^*)}{dt} = -\delta(t)P(t, \phi^*) \quad \text{for all } t \geq \tau.$$

It follows that $P(t, \phi^*) \rightarrow 0$ as $t \rightarrow \infty$, which contradicts $P(t, \phi^*) \geq \min_{t \in [0, \omega]} P(t, \phi^*) > 0$ for all $t \geq 0$, validating the claim.

Since

$$\begin{aligned} \frac{dB(t, \phi^*)}{dt} &\geq -\frac{r(t)B(t, \phi^*)^2}{K(t)} - \frac{\gamma(t)B(t, \phi^*)P(t, \phi^*)}{K_1(t) + B(t, \phi^*)} \\ &\geq -\left(\frac{r(t)\max_{t \in [0, \omega]} B(t, \phi^*)}{K(t)} + \frac{\gamma(t)\max_{t \in [0, \omega]} P(t, \phi^*)}{K_1(t)}\right) B(t, \phi^*), \end{aligned}$$

it follows that $B(t, \phi^*) > 0$ for all $t \geq \bar{t}$. The periodicity of $B(t, \phi^*)$ implies that $B(t, \phi^*) > 0$ for all $t \geq 0$. Therefore, $(B(t, \phi^*), P(t, \phi^*))$ is a positive ω -periodic solution of system (2).

By Theorem 4.5 of [36] with $\rho(x) = d(x, \partial X_0)$, it then follows that $Q: X_0 \rightarrow X_0$ has a compact global attractor A_0 . For any $\phi = (\phi_1, \phi_2) \in A_0$, we have $\phi_2(0) > 0$. Let $B_0 := \bigcup_{t \in [0, \omega]} Q(t)A_0$. Then $\psi_2(0) > 0$ for all $\psi = (\psi_1, \psi_2) \in B_0$. Moreover, $B_0 \subseteq X_0$ and $\lim_{t \rightarrow \infty} d(Q(t)\phi, B_0) = 0$ for all $\phi \in X_0$. Define a continuous function $\bar{p}: X \rightarrow \mathbb{R}_+$ by

$$\bar{p}(\phi) = \phi_2(0), \quad \forall \phi \in X.$$

Since B_0 is a compact subset of X_0 , we have $\inf_{\phi \in B_0} \bar{p}(\phi) = \min_{\phi \in B_0} \bar{p}(\phi) > 0$. Consequently, there exists $\bar{\eta} > 0$ such that

$$\liminf_{t \rightarrow \infty} P(t, \phi) = \liminf_{t \rightarrow \infty} \bar{p}(Q(t)\phi) \geq \bar{\eta}.$$

From the proof of Lemma 1, we see that there exists $T_1 > 0$ such that $B(t) < x^*$ for all $t \geq T_1$, and that there exists $T_2 > 0$ such that $P(t) \leq \hat{K}$ for all $t \geq T_2$ (see (8) for the expression of \hat{K}). Let $T = \max\{T_1, T_2\}$. It then follows that

$$\begin{aligned} \frac{dB(t)}{dt} &\geq -\frac{r(t)B(t)^2}{K(t)} - \frac{\gamma(t)B(t)P(t)}{K_1(t) + B(t)} \\ &\geq -\left(\frac{r(t)x^*}{K(t)} + \frac{\gamma(t)\hat{K}}{K_1(t)}\right) B(t) \quad \text{for all } t \geq T. \end{aligned} \tag{6}$$

For any $\phi \in X_0$, we claim that there exists $t_0 \geq T$ such that $B(t_0, \phi) > 0$. Otherwise, $B(t, \phi) \equiv 0$ for all $t \geq T$. Then from the second equation of system (2), we have $\lim_{t \rightarrow \infty} P(t, \phi) = 0$, which contradicts $\liminf_{t \rightarrow \infty} P(t, \phi) \geq \bar{\eta}$.

From (6) we get

$$B(t, \phi) \geq \exp\left\{-\int_{t_0}^t \left(\frac{r(s)x^*}{K(s)} + \frac{\gamma(s)\hat{K}}{K_1(s)}\right) ds\right\} B(t_0, \phi) > 0$$

for all $t \geq t_0$.

Fix n such that $n\omega > t_0$. Then for $\psi \in A_0$, we have $B(n\omega, \psi) > 0$. By the invariance of A_0 , we have $A_0 = Q^n(A_0) = Q(n\omega)A_0$. It follows that for $\phi \in A_0$, there exists $\psi \in A_0$ such that $\phi = Q(n\omega)\psi$. Thus, $\phi_1(0) = B(n\omega, \psi) > 0$. Then we can define a continuous function $p: X \rightarrow \mathbb{R}_+$ by

$$p(\phi) = \min\{\phi_1(0), \phi_2(0)\}, \quad \forall \phi \in X.$$

Since B_0 is a compact subset of X_0 , we have $\inf_{\phi \in B_0} p(\phi) = \min_{\phi \in B_0} p(\phi) > 0$. Consequently, there exists $\eta > 0$ such that

$$\liminf_{t \rightarrow \infty} \min\{B(t, \phi), P(t, \phi)\} = \liminf_{t \rightarrow \infty} p(Q(t)\phi) \geq \eta.$$

This completes the proof of Theorem 1. \square

4. Numerical experiments

In this section, we use the *Daphnia*-algae interaction as an example to numerically verify the obtained analytic result and explore the mechanisms for seasonal population cycles. One of the most distinctive phenomena in plankton communities is an early spring bloom of algae followed by a peak of zooplankton grazing down algal biomass resulting in the spring clear-water phase around early June [38]. The algal bloom can be caused in part by depletion of the available nutrients [39,40], but heavy grazing on algae by zooplankton species that peak after the spring algal bloom is usually the main mechanism causing the clear-water phase [41,42].

4.1. Model validation

In this section, we fit our model to the monthly mean algae data from 1998 to 2008 in Bohai Sea by using the least squares method. Fig. 3 of [43] shows obvious seasonal fluctuations of Chlorophyll *a* density in Bohai Sea from 1998 to 2008. Since Chlorophyll *a* constitutes about 1% to 2% of the dry weight of planktonic algae [44], we estimate the algae density in Bohai Sea by dividing the Chlorophyll *a* density by 1.5%. The estimated algae density in Bohai Sea are displayed by the red stars in Fig. 1. The eggs produced by female *Daphnia* usually hatch after a day, and remain in the female's brood pouch for around three days (at 20 °C). They are then released into the water, and go through 4 to 6 instars over 5 to 10 days (longer in poor conditions) before reaching an

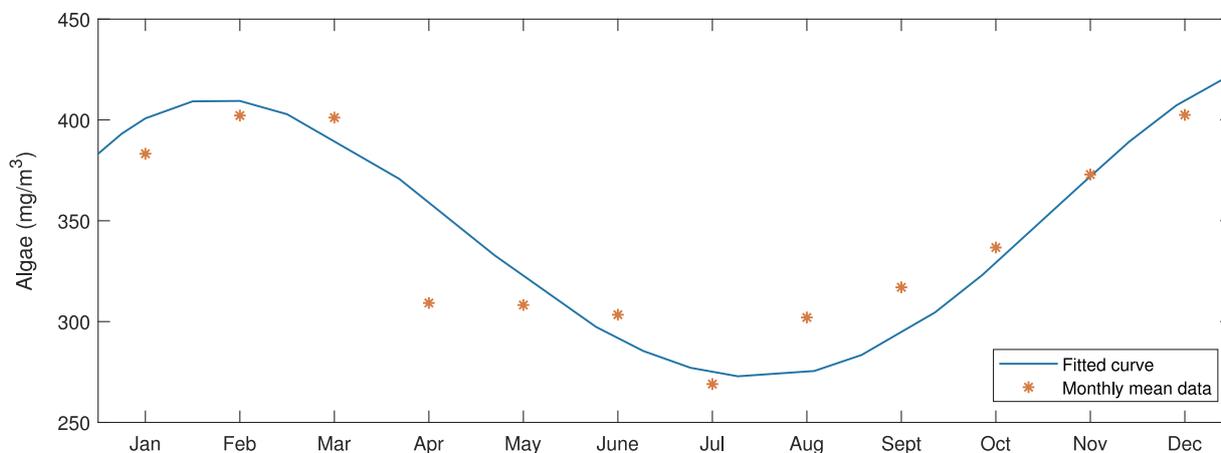


Fig. 1. Comparison of the fitted curve and the monthly mean algae data from 1998 to 2008 in Bohai Sea.

Table 2

Parameter values estimated from Tan et al. [43].

Parameter	Values	Description	Units
r	0.9996	Time-averaged maximum per capita growth rate of algae	month ⁻¹
K	351.6521	Time-averaged carrying capacity for algae	mg/m ³
γ	0.0391	Maximum per capita predation rate of <i>Daphnia</i>	month ⁻¹
K_1	505.6108	Half-saturation constant of <i>Daphnia</i> 's functional response	
β	58.8442	Conversion rate from algae biomass to <i>Daphnia</i> biomass	
δ	0.9357	<i>Daphnia</i> death rate	month ⁻¹
τ	0.5	<i>Daphnia</i> maturation delay	month

age at which they are able to reproduce [45]. Thus, it is reasonable to assume that τ is around 0.5 month in our model. Considering that seasonality has a strong effect on the growth rate and the carrying capacity of the algae population, we assume that $r(t)$ and $K(t)$ are periodic functions given by $r(t) = r + \frac{r}{4} \cos(\frac{2\pi t}{12})$, $K(t) = K + \frac{K}{4} \cos(\frac{2\pi t}{12})$, and keep all the other parameters constant. For simplicity, we assume that $\delta_j(t) = \delta(t) = \delta$ in our simulation. The estimated parameter values are given in Table 2 and the fitting result is shown in Fig. 1. Note that our estimation is based on algae data only. The algae data together with different data of *Daphnia* would probably return different parameter values. To give a more accurate estimation of the parameters we need time series data of both algae and *Daphnia* from field ecologists. In the following simulation, we will use parameter values close to the estimated values in Table 2.

4.2. Long-term dynamics

To numerically calculate R_0 , we use Theorem 2.2 of [19], Lemma 2.5 of [46] and the bisection method. Using the parameter values in Table 2 and setting $\gamma = 0.06$ and $\tau = 0.4$, we obtain $R_0 = 1.0711$. In this case, both algae and *Daphnia* densities have seasonal fluctuations as shown in Fig. 2 (a). In Fig. 2 (b), we decrease the value of γ to 0.02 and increase the value of τ to 0.5. We observe that the algae density fluctuates seasonally and the *Daphnia* density approaches 0 eventually. In this case, $R_0 = 0.3251$.

4.3. The role of seasonality

To determine whether it is seasonality that produces the seasonal fluctuation of algae and daphnia densities, we discard seasonality in our model by setting $r(t) = 0.9996$ and $K(t) = 351.6521$ and keep the values of other parameters the same as those in Fig. 2 (a). We obtain $R_0 = 1.0646$ and we observe that the solution approaches a positive coexistence equilibrium in Fig. 3 (a). After we decrease the value of γ to 0.02 and increase the value of τ to 0.5, we got $R_0 = 0.3232$ and the

solution approaches a *Daphnia*-free equilibrium in Fig. 3 (b). Fig. 3 indicates that seasonal fluctuations cannot be observed for the *Daphnia*-algae system if we do not incorporate seasonality in the model. Thus, the seasonal cycles of the *Daphnia*-algae system is caused by seasonality rather than *Daphnia* maturation delay or *Daphnia*-algae interaction.

Next we explore how the amplitudes of the periodic parameters $r(t)$ and $K(t)$ affect the amplitude of the solutions. Since $r(t) = r + \frac{r}{4} \cos(\frac{2\pi t}{12})$ and $K(t) = K + \frac{K}{4} \cos(\frac{2\pi t}{12})$, the amplitudes of $r(t)$ and $K(t)$ are $\frac{r}{4}$ and $\frac{K}{4}$, respectively. Thus, we can investigate the role of the amplitudes of $r(t)$ and $K(t)$ by varying the values of r and K . From Fig. 4 we see that the amplitudes of the *Daphnia*-algae fluctuations increase as the amplitude of $r(t)$ increases. Besides, the average *Daphnia* density level obviously increases as the amplitude of $r(t)$ increases. Similarly, Fig. 5 shows that the amplitudes of the *Daphnia*-algae fluctuations also increase as the amplitude of $K(t)$ increases.

4.4. The role of maturation delay

The duration of the *Daphnia* maturation delay is greatly affected by environmental factors. In this section we study the role of *Daphnia* maturation delay in determining R_0 and the amplitude of fluctuations. Fig. 6 shows that R_0 is a decreasing function of τ . This implies that shortening maturation delay is a favoured strategy for the *Daphnia* population to persist. In Fig. 7, we plot long-term dynamics of algae and *Daphnia* densities using several different values of τ . In Fig. 7 (a) and (b) where $R_0 > 1$ for all the cases, we see that the amplitude of the algae fluctuation decreases and the average algae density level increases as τ increases. Both the amplitude of the *Daphnia* fluctuation and the average *Daphnia* density level decrease as τ increases. In Fig. 7 (c) and (d) where $R_0 < 1$, the algae and *Daphnia* densities approach the *Daphnia*-free periodic fluctuation state. In addition, the algae population approaches the periodic cycle faster and the *Daphnia* population goes extinct faster if τ is larger.

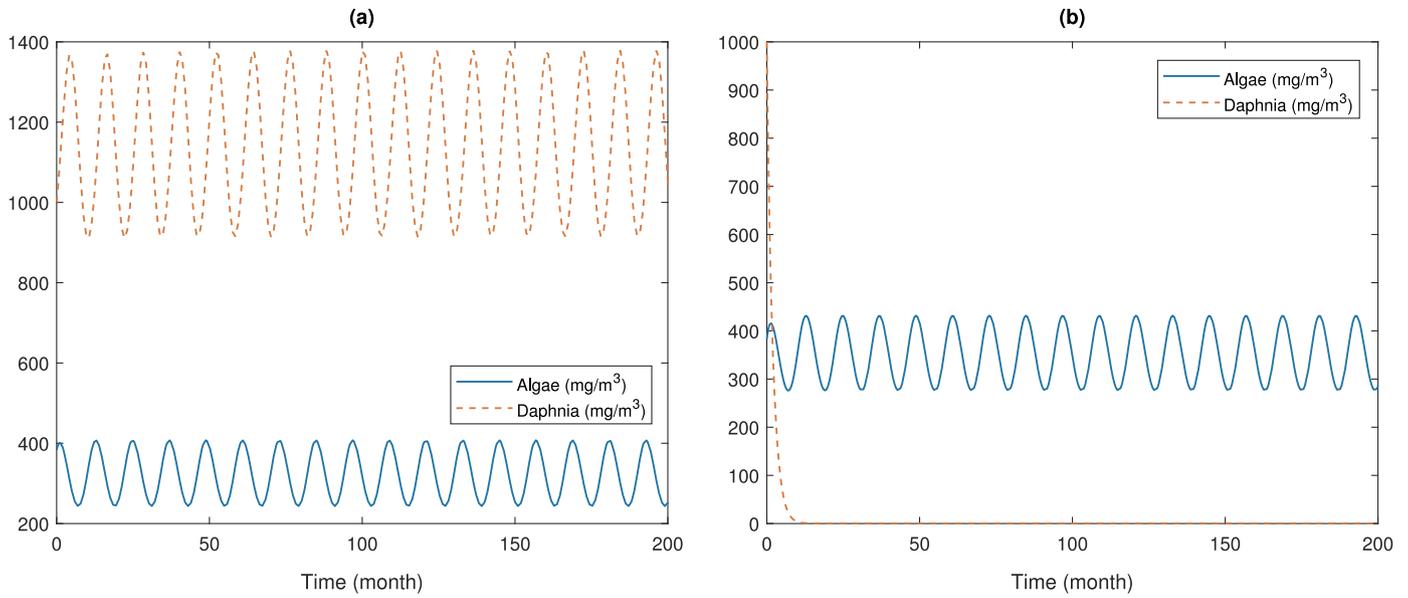


Fig. 2. Long-term behavior of the solutions. (a) $\gamma = 0.06$, $\tau = 0.4$, $R_0 = 1.0711$. (b) $\gamma = 0.02$, $\tau = 0.5$, $R_0 = 0.3251$. The other parameter values are $r(t) = 0.9996 + \frac{0.9996}{4} \cos(\frac{2\pi t}{12})$, $K(t) = 351.6521 + \frac{351.6521}{4} \cos(\frac{2\pi t}{12})$, $K_1 = 505.6108$, $\beta = 58.8442$, $\delta = 0.9357$.

4.5. Sensitivity analysis

The objective of this section is to discuss the sensitivity of the basic reproduction ratio to model parameters. To do this, we use the normalized forward sensitivity index (see [47]):

$$\text{Sensitivity index (S.I.)} = \frac{\partial R_0}{\partial(\text{parameter})} \cdot \frac{\text{parameter}}{R_0}. \tag{7}$$

Since R_0 cannot be written as an explicit function of parameters, we use the central difference approximation to evaluate the derivatives (see [48]):

$$\frac{\partial R_0}{\partial(\text{parameter})} = \frac{R_0(\text{parameter} + h) - R_0(\text{parameter} - h)}{2h} + O(h^2).$$

Letting $h = 1\%$ of the parameter value (P), Eq. (7) becomes

$$\text{S.I.} = \frac{R_0(1.01P) - R_0(0.99P)}{0.02R_0(P)}.$$

Using this formula we obtain that the sensitivity indices of R_0 to parameters τ , γ , β , K_1 , δ , r and K are -0.4678 , 0.9973 , 0.9973 , -0.5912 , -1.4651 , 0 and 0.5963 , respectively (see Fig. 8).

In Fig. 8, we fixed the parameter values when we calculated the sensitivity indices. However, the sensitivity indices may vary as some of the parameters vary. Next, we investigate the sensitivity indices of R_0 to some important parameters in different parameter domains. In Fig. 9 (a), we see that the sensitivity index of R_0 to K is positive and increases as K decreases. It almost has no response to the variation in τ . However, the sensitivity of R_0 to τ is greatly influenced by the value of τ instead of K . As can be seen from Fig. 9 (b), the sensitivity index of R_0 to τ is negative and decreases as τ increases, which means that R_0 is more sensitive to τ for larger values of τ . The sensitivity index of R_0 to γ approximately equals one for all positive values of $\gamma \in (0, 0.2]$ and

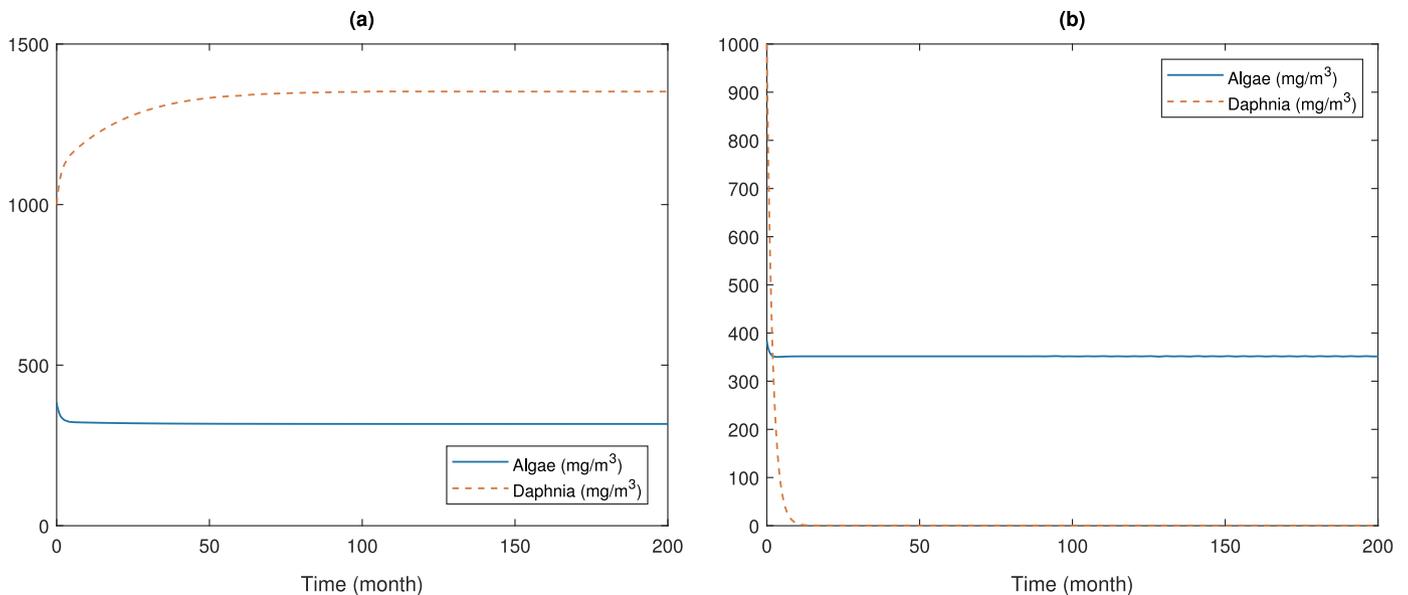


Fig. 3. Long-term behavior of the solutions. (a) $\gamma = 0.06$, $\tau = 0.4$, $R_0 = 1.0646$. (b) $\gamma = 0.02$, $\tau = 0.5$, $R_0 = 0.3232$. The other parameter values are $r(t) = 0.9996$, $K(t) = 351.6521$, $K_1 = 505.6108$, $\beta = 58.8442$, $\delta = 0.9357$.

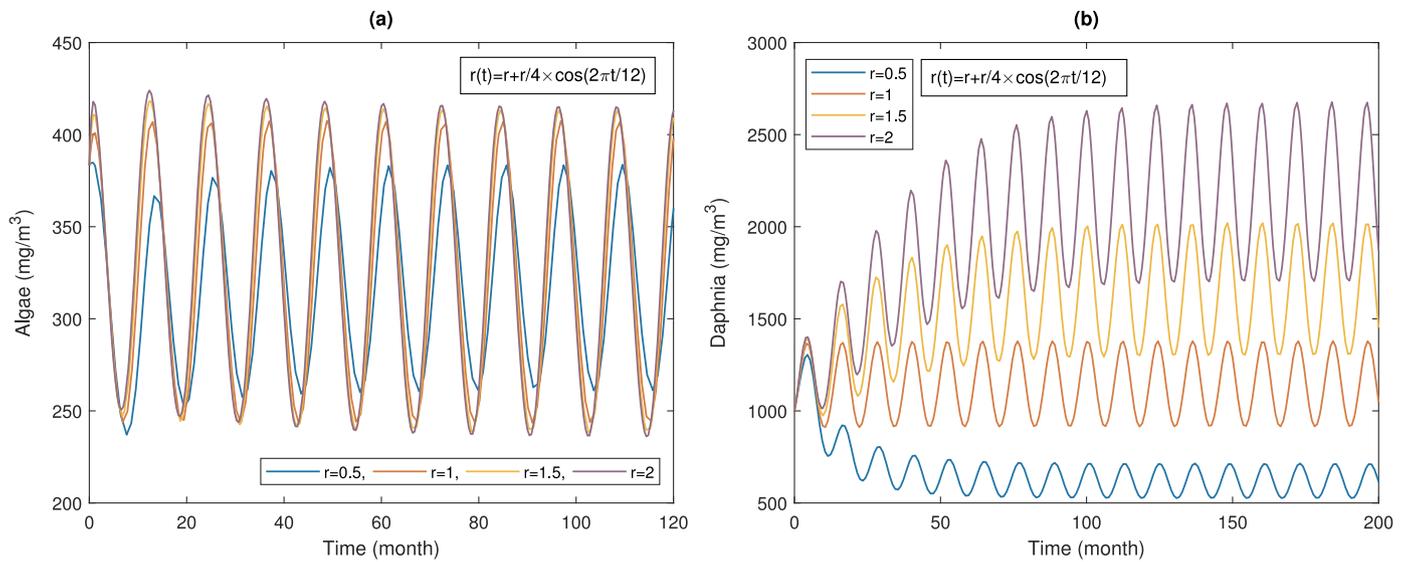


Fig. 4. The role of the amplitude of $r(t)$ in determining the amplitude of the fluctuations. (a) Algae dynamics. (b) *Daphnia* dynamics. Here $r(t) = r + \frac{r}{4} \cos(\frac{2\pi t}{12})$ with $r = 0.5, 1, 1.5, 2$. Other parameter values are $K(t) = 351.6521 + \frac{351.6521}{4} \cos(\frac{2\pi t}{12})$, $\gamma = 0.06$, $K_1 = 505.6108$, $\beta = 58.8442$, $\delta = 0.9357$, $\tau = 0.4$.

$K \in [150, 800]$ as shown in Fig. 9 (c). Fig. 9 (d) shows that the sensitivity index of R_0 to δ is negative and decreases as δ and τ increase. The sensitivity result is summarized in Table 3.

5. Discussion

The stimulus for our work is the coexistence and seasonal fluctuations of some predator and prey species in nature. Multi-year oscillations in small mammal populations such as lemmings and snowshoe hares have been a constant attraction and inspiration for ecologists. However, the study of coexistence and seasonal oscillations in other species seems to have received much less attention in predator-prey models. We addressed this issue by developing and analyzing a predator-prey model that incorporates seasonality and predator maturation delay simultaneously. By using the comparison method and the theory of uniform persistence, we obtained the threshold dynamics of the model in terms of the basic reproduction ratio R_0 , which is defined as the spectral radius of a linear operator. From the formulation of the linear operator, it is clear to see that R_0 depends on all parameters. The

role of R_0 in our model is similar to that of the basic reproduction number in infectious disease models if we treat prey as susceptibles and predators as infectives. According to our result, whether predators can coexist with prey exclusively depends on whether R_0 is greater than one. The prey have seasonal oscillations whereas the predators become extinct when $R_0 < 1$. The predators can coexist with prey and both prey and predators fluctuate seasonally when $R_0 > 1$. The method presented in this paper can be employed to prove the uniform persistence of some other systems of periodic delay differential equations. As a case study, we applied our model to the *Daphnia*-algae interaction in a natural environment. The simulated long-term dynamics of the *Daphnia*-algae system verified the analytic result. Seasonal dynamics of the *Daphnia*-algae system is found to be governed by seasonality rather than other factors in the model. The *Daphnia* maturation delay only affects the amplitude of cycles and average population levels. Sensitivity analysis identified the key parameters that could possibly determine the basic reproduction ratio. Although the simulations in this paper are based on *Daphnia*-algae system, the model and the analytic approach are general and apply to other predator-prey, consumer-resource and host-parasite

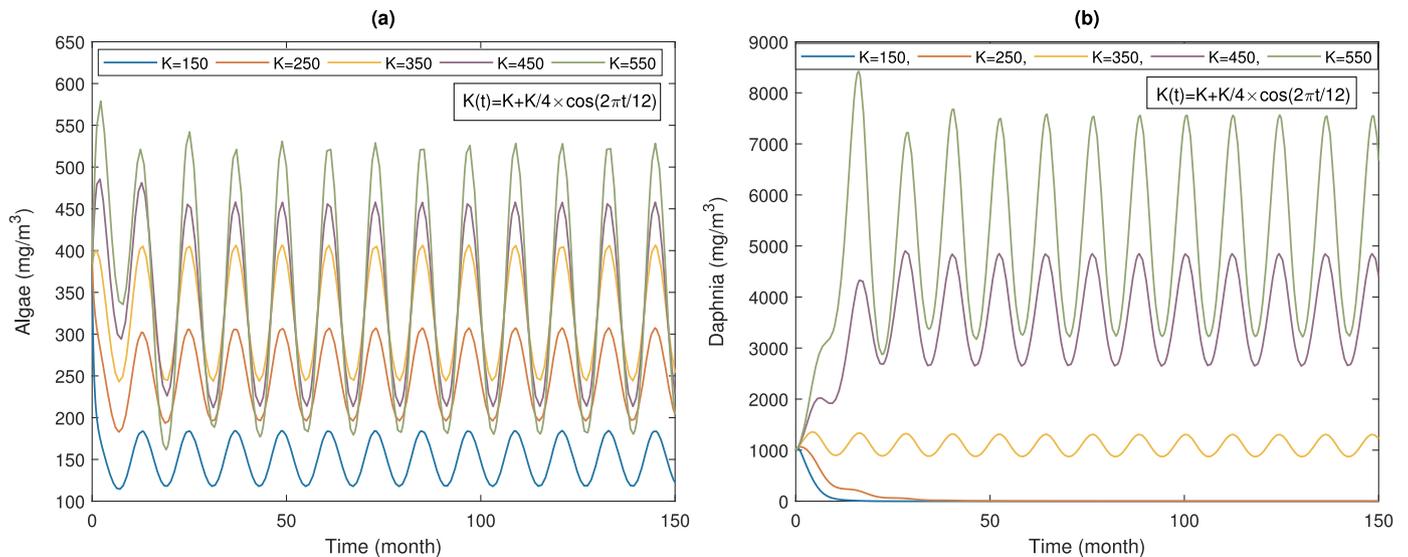


Fig. 5. The role of the amplitude of $K(t)$ in determining the amplitude of the fluctuations. (a) Algae dynamics. (b) *Daphnia* dynamics. Here $K(t) = K + \frac{K}{4} \cos(\frac{2\pi t}{12})$ with $K = 150, 250, 350, 450, 550$. Other parameter values are $r(t) = 0.9996 + \frac{0.9996}{4} \cos(\frac{2\pi t}{12})$, $\gamma = 0.06$, $K_1 = 505.6108$, $\beta = 58.8442$, $\delta = 0.9357$, $\tau = 0.4$.

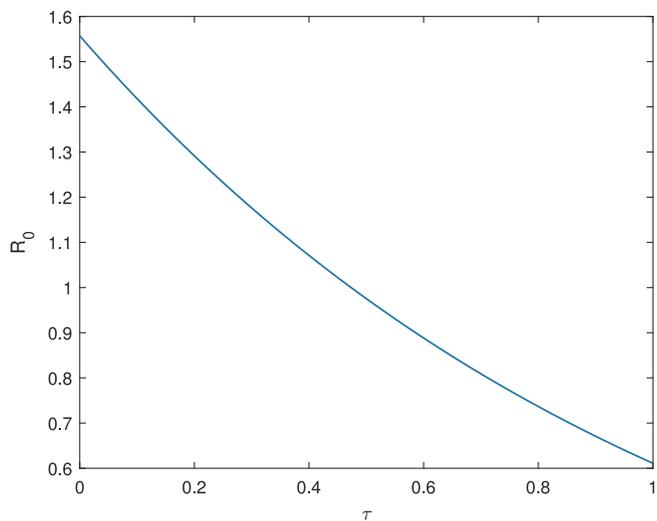


Fig. 6. R_0 as a function of τ . Here $\gamma = 0.06$, $K_1 = 505.6108$, $\beta = 58.8442$, $\delta = 0.9357$, $r(t) = 0.9996 + \frac{0.9996}{4} \cos(\frac{2\pi t}{12})$, $K(t) = 351.6521 + \frac{351.6521}{4} \cos(\frac{2\pi t}{12})$.

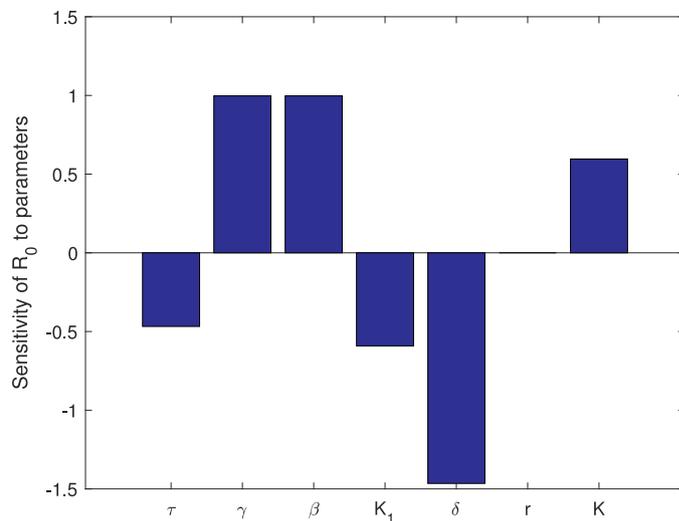


Fig. 8. Sensitivity of R_0 to parameters. The parameter values used in the computation of sensitivity indices are $\gamma = 0.06$, $K_1 = 505.6108$, $\beta = 58.8442$, $\delta = 0.9357$, $r(t) = r + \frac{r}{4} \cos(\frac{2\pi t}{12})$, $K(t) = K + \frac{K}{4} \cos(\frac{2\pi t}{12})$, where $r = 0.9996$, $K = 351.6521$.

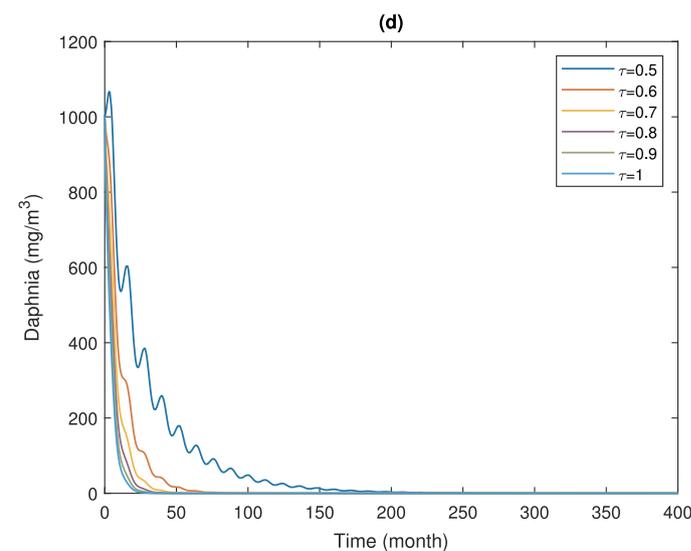
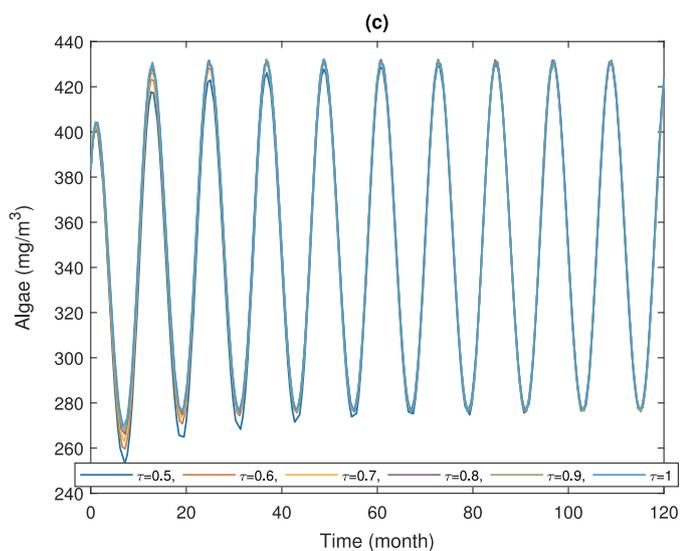
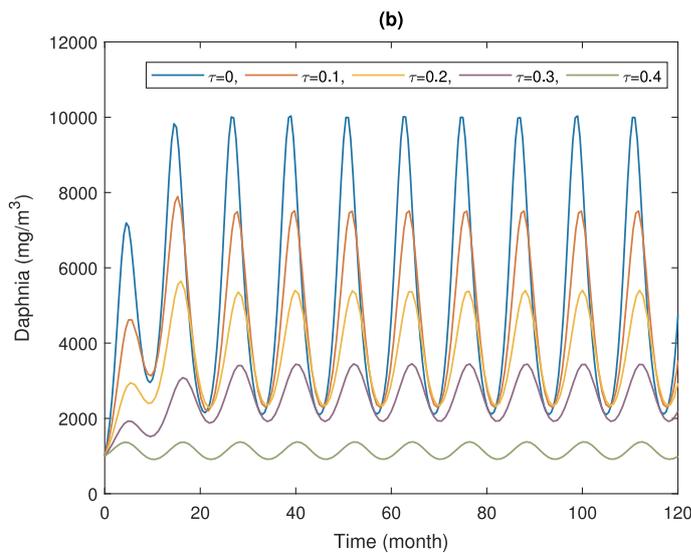
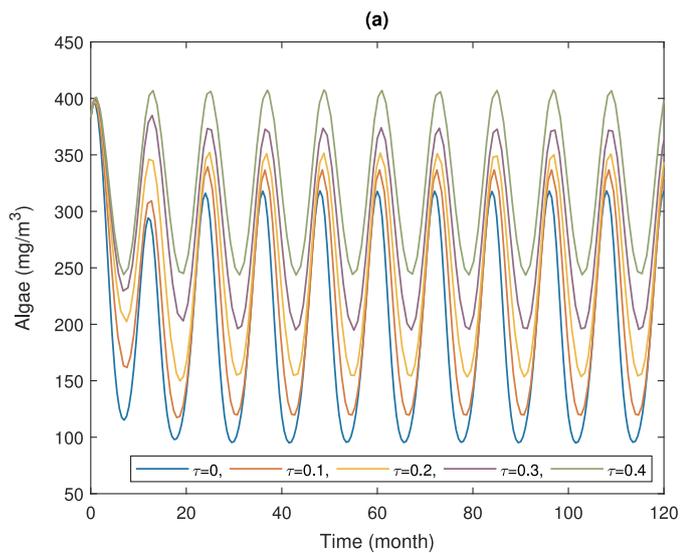


Fig. 7. The role of maturation delay in population cycles. All parameter values are the same as those in Fig. 6 except τ . (a) Algae dynamics. τ varies from 0 to 0.4. (b) *Daphnia* dynamics. τ varies from 0 to 0.4. (c) Algae dynamics. τ varies from 0.5 to 1. (d) *Daphnia* dynamics. τ varies from 0.5 to 1.

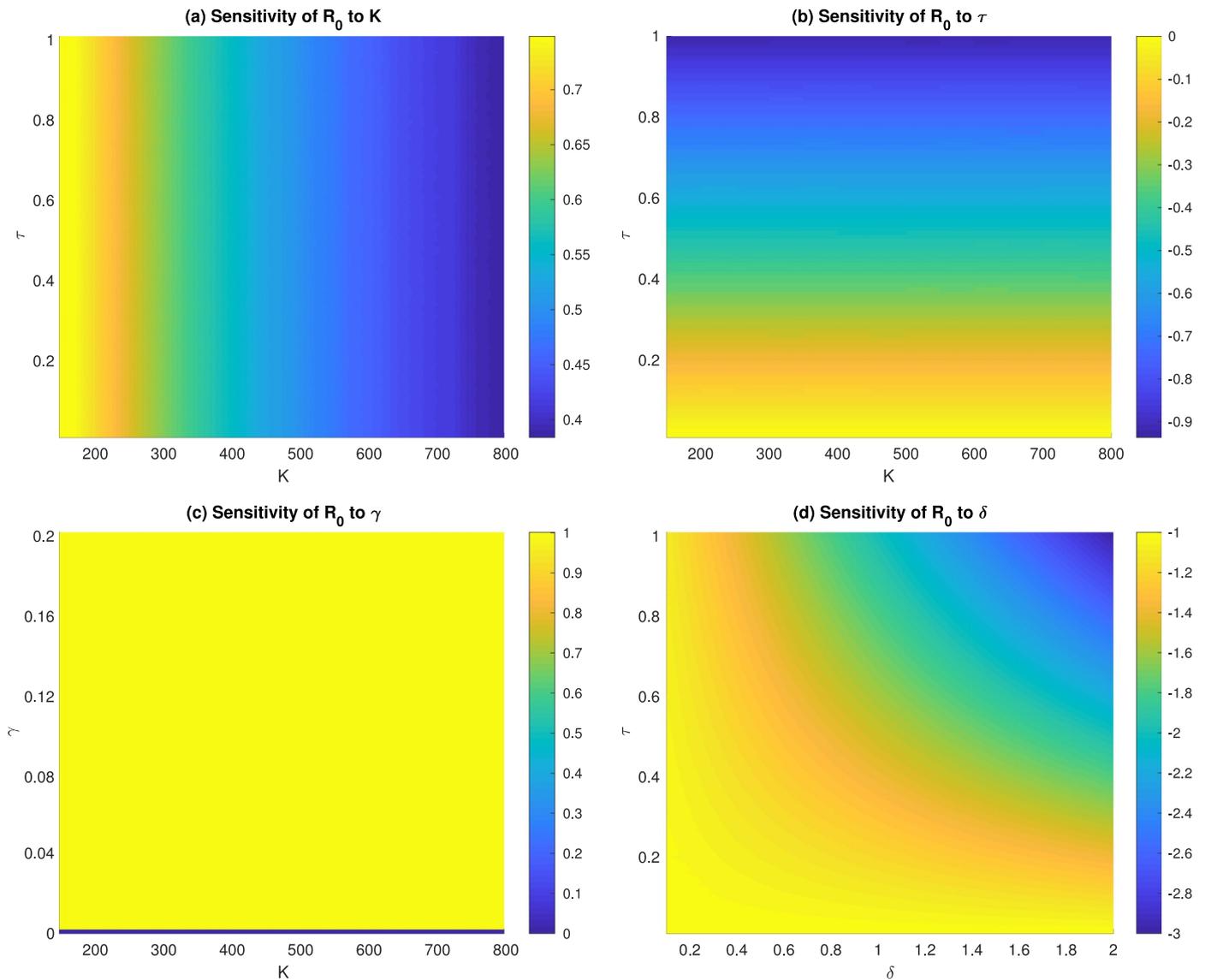


Fig. 9. (a) Sensitivity of R_0 to K as K varies from 150 to 800 and τ varies from 0 to 1. (b) Sensitivity of R_0 to τ as K varies from 150 to 800 and τ varies from 0 to 1. (c) Sensitivity of R_0 to γ as K varies from 150–800 and γ varies from 0 to 0.2. (d) Sensitivity of R_0 to δ as δ varies from 0 to 2 and τ varies from 0 to 1. Other parameter values are the same as those in Fig. 8.

Table 3
Sensitivity of R_0 to parameters in different parameter domains.

Sensitivity of R_0 to	Parameter domain	Sensitivity	Sensitive region
K	(K, τ)	positive	K small
τ	(K, τ)	negative	τ large
γ	(K, γ)	positive	γ positive
δ	(δ, τ)	negative	δ large, τ large

systems in which life-history parameters change seasonally and delay matters.

Several previous studies of predator-prey models indicated that predator maturation delay was a potential mechanism that generated multi-year population cycles in some mammalian species [27], but left unknown whether it was also the maturation delay that caused seasonal fluctuations in some other species. By investigating the autonomous system which is derived by discarding seasonality in our model, we found that seasonal cycles of *Daphnia* and algae populations are caused by seasonality. Our observations suggest that, at least for *Daphnia*-algae interaction, predator maturation delay only affects the amplitude and

average population levels. The delay could not determine the period of seasonal population cycles as it did for the multi-year cycles of mammalian predator-prey systems. Thus, our work indicates that seasonality should not be ignored when we develop models for predator-prey interactions that are strongly affected by seasonal factors and exhibit obvious seasonal fluctuations in nature.

It is important to study the impact of climate factors on the dynamics of predator-prey systems with the advance of global warming. In the numerical simulations, we simply take the growth rate and carrying capacity of algae population as sinusoidal functions. More complicated functions may be needed to represent the periodic parameters in some cases. Currently, for some predator-prey systems, data are available only for prey but not for predators or conversely. On the other hand, most data are collected in a particular season not for consecutive years. For a more in-depth understanding of the effects of seasonal factors on the dynamics of predator-prey systems, more complete region-specific data about different predator and prey species from field ecology is of paramount importance.

The predator maturation delay in our model is a constant parameter. Indeed, the delay can depend on prey availability or some other

external environmental factors. We can modify our model such that the delay is a function of prey density or seasonal factors. With the parameter values used in this paper, seasonal cycles are not observed for the model without seasonality. It is of interest to investigate whether the autonomous model can have ω -periodic cycles with other sets of validated parameter values. For the case $R_0 > 1$, we only proved the existence of an ω -periodic solution. It is interesting to study whether the ω -periodic solution is unique and whether there are other periodic solutions whose periods are not the same as the period of the parameters. We leave this for future investigation.

Appendix

Proof of Lemma 1.

Proof. For any $\varphi \in C^+$, define

$$f(t, \varphi) = \left(\begin{array}{l} r(t)\varphi_1(0)\left(1 - \frac{\varphi_1(0)}{K(t)}\right) - \gamma(t)\frac{\varphi_1(0)}{K_1(t) + \varphi_1(0)}\varphi_2(0) \\ \beta\gamma(t - \tau)e^{-\int_{t-\tau}^t \delta_j(s)ds} \frac{\varphi_1(-\tau)}{K_1(t-\tau) + \varphi_1(-\tau)}\varphi_2(-\tau) - \delta(t)\varphi_2(0) \end{array} \right).$$

Then f is continuous in $(t, \varphi) \in \mathbb{R}_+ \times C^+$, and f is Lipschitz in φ on each compact subset of C^+ . It follows that system (2) has a unique solution $u_i(\varphi) = u_i(t, \varphi)$ with $u_0 = \varphi$ on its maximal interval $[0, \sigma_\varphi)$ of existence (see Theorems 2.2.1 and 2.2.3 of [32]).

Let $\varphi = (\varphi_1, \varphi_2) \in C^+$ be given. If $\varphi_i(0) = 0$, then $f_i(t, \varphi) \geq 0, i = 1, 2$. By Theorem 5.2.1 of [33], it follows that the unique solution $u(t, \varphi)$ of system (2) with $u_0 = \varphi \in C^+$ satisfies $u_i(\varphi) \in C^+$ for all $t \in [0, \sigma_\varphi)$.

The first equation of system (2) implies that $\frac{dB(t)}{dt} \leq r(t)B(t)\left(1 - \frac{B(t)}{K(t)}\right)$. Since the equation $\frac{dx(t)}{dt} = r(t)x(t)\left(1 - \frac{x(t)}{K(t)}\right)$ has a globally attractive positive ω -periodic solution $x^*(t)$, by the comparison principle, there exists $T_1 > 0$ such that

$$B(t) < \max_{t \in [0, \omega]} x^*(t) + 1 := x^* \text{ for all } t \geq T_1.$$

Let $z(t) = \beta e^{-\int_t^{t+\tau} \delta_j(s)ds} B(t) + P(t + \tau)$ and $K^* = \max\{\max_{t \in [0, \omega]} K(t), x^*\}$. Then

$$\begin{aligned} \frac{dz(t)}{dt} &= \beta e^{-\int_t^{t+\tau} \delta_j(s)ds} \left[r(t)B(t)\left(1 - \frac{B(t)}{K(t)}\right) - \frac{\gamma(t)B(t)P(t)}{K_1(t) + B(t)} \right] \\ &\quad + \beta e^{-\int_t^{t+\tau} \delta_j(s)ds} B(t)[\delta_j(t) - \delta_j(t + \tau)] \\ &\quad + \beta e^{-\int_t^{t+\tau} \delta_j(s)ds} \frac{\gamma(t)B(t)P(t)}{K_1(t) + B(t)} - \delta(t + \tau)P(t + \tau) \\ &\leq \beta e^{-\int_t^{t+\tau} \delta_j(s)ds} r(t)K^*\left(1 - \frac{B(t)}{K^*}\right) + \beta K^* e^{-\int_t^{t+\tau} \delta_j(s)ds} \delta_j(t) \\ &\quad - \delta(t + \tau)P(t + \tau) \\ &\leq \beta K^* e^{-\int_t^{t+\tau} \delta_j(s)ds} (r(t) + \delta_j(t)) - \min_{t \in [0, \omega]} \{r(t), \delta(t + \tau)\} z(t) \end{aligned}$$

for all $t \geq T_1$. It follows that

$$\limsup_{t \rightarrow \infty} z(t) \leq \frac{\max_{t \in [0, \omega]} \{\beta K^* e^{-\int_t^{t+\tau} \delta_j(s)ds} (r(t) + \delta_j(t))\}}{\min_{t \in [0, \omega]} \{r(t), \delta(t + \tau)\}},$$

and hence,

$$\limsup_{t \rightarrow \infty} P(t) \leq \frac{\max_{t \in [0, \omega]} \{\beta K^* e^{-\int_t^{t+\tau} \delta_j(s)ds} (r(t) + \delta_j(t))\}}{\min_{t \in [0, \omega]} \{r(t), \delta(t + \tau)\}} := \hat{K}. \tag{8}$$

□

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