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PERIODIC SOLUTIONS OF SINGLE-SPECIES MODELS WITH PERIODIC DELAY*

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Abstract. A single-species population growth model is considered, where the growth rate response to changes in its density has a periodic delay. It is shown that if the self-inhibition rate is sufficiently large compared to the reproduction rate, then the model equation has a globally asymptotically stable positive periodic solution.

Key words. single-species, population growth, oscillations, periodic solutions, delay equations, global stability, fixed point theorems

AMS(MOS) subject classifications. 92A17, 34K20

1. Introduction. The main focus of this paper is on a model of single-species population growth which incorporates a periodic time delay in the birth process. In particular, we show the existence of a stable periodic solution of a retarded functional differential equation to be given later which has the feature of periodicity right in the time delay. To the best of our knowledge, this is the first time equations with such delays have been considered in the literature.

This paper is motivated by the laboratory work of the group led by U. Halbach (see [4], [21]-[24], [40], [44] and the references therein) on rotifers. They noticed that in laboratory populations, periodic phenomena due to time delays in gestation occurred, and that the length of delay was a function of the controlled temperature. These periodic variations in population numbers also occurred when the temperature itself was varied periodically (thereby inducing a periodic delay) on a daily basis. This led us to a conjecture that periodic solutions should exist for single species delay models with periodic delay.

Previous work has shown that periodic oscillations could occur in autonomous delay differential equations [5], [6], [10], [13], [15], [16], [20], [25], [29]-[31], [35], [37], [40], [43], [45], as well as delay equations for population growth in fluctuating environments [2], [9], [11], [12], [14], [19], [28], [32]-[34], [39], [45]. However, periodic oscillations are not automatic in single-species models with delay as shown in [3], [7], [8], [18].

In the case where the delay in growth rate is a constant, the mechanism causing oscillation is for the delay to be so significant in terms of the time length of the delay or the magnitude of the delayed effects that the positive equilibrium point (carrying capacity) loses its stability. For details, we refer to [13] and the references therein.

The technique used in the analysis of our model is to first show that due to the periodicity of the growth rate and of the delay, there exists a positive periodic carrying capacity which is not a solution, but yields a globally stable periodic oscillation in the species density. In contrast with the aforementioned research for the constant delay case, we find that the periodicity in various growth rates and in the delay can cause stable oscillation of the species density about the carrying capacity even when the delay is small.

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The idea here is to then treat the periodic oscillation as being generated from the periodic carrying capacity by proving the existence of an attracting region containing the carrying capacity.

The organization of this paper is as follows. Model equations and our major results are described in § 2. We will state our results for the linear growth rate case in detail and briefly indicate the possible extension to the nonlinear growth rate case. The proofs of the theorems are contained in § 3. Under the assumption of the existence of a periodic carrying capacity, we construct a Lyapunov function about the carrying capacity and employ the Lyapunov-Razumikhin technique to obtain an attracting region. Section 4 contains a brief discussion of our results and some related open problems.

2. Model equations and main results.

2.1. Linear growth rates. We first consider the following single-species model involving a discrete periodic delay

$$\dot{x}(t)=x(t)[a(t)-b(t)x(t)+c(t)x(t-\tau(t))], \tag{2.1}$$

where the net birth rate $a(t)$, the self-inhibition rate $b(t)$, the reproduction rate $c(t)$, and the delay $\tau(t)$ are continuously differentiable, ω-periodic functions, and $a(t)>0$, $b(t)>0$, $c(t)\geqq 0$, $\tau(t)\geqq 0$ for $t\in R=(-\infty,+\infty)$. This model represents the case that when the population size is small, growth is proportional to the size, and when the population size is not so small, the positive feedback is $a(t)+c(t)x(t-\tau(t))$ while the negative feedback is $b(t)x(t)$. Such circumstances can arise when the resources are plentiful and the reproduction at time t is by individuals of at least age $\tau(t)$ units of time.

The above model, with constant coefficient and delay, and its variants, has been utilized by many authors as a model of single species growth (see [18] and the references therein). The delay in the term $c(t)x(t)x(t-\tau(t))$ is a delay due to gestation. Thinking of small animals such as rotifers (as in the work of Halbach and co-workers mentioned in the introduction), there is a small delay in the time between final feeding before reproduction and reproduction. Hence, the reproduction rate has a component which is proportional to those animals present a short time earlier and those animals currently present (random mating).

Let $\tau^*=\max_{t\in[0,\omega]}\tau(t)$. It is a well-known fact that for any given $\varphi\in C([-\tau^*,0];R)$, there exist $\alpha\in(0,\infty)$ and a unique solution $x(t)=x(t;\varphi)$ of (2.1) on $[-\tau^*,\alpha)$; that is, $x(t)$ is continuous on $[-\tau^*,\alpha)$, continuously differentiable, and satisfies (2.1) on $(0,\alpha)$ and $x(\theta)=\varphi(\theta)$ on $[-\tau^*,0]$. Moreover, if $\varphi(t)\geqq 0$ on $[-\tau^*,0]$, then $x(t)$ remains nonnegative for all $t\in[0,\alpha)$, and if x is noncontinuable past α and $\alpha<+\infty$, then $|x(t)|\to\infty$ as $t\to\alpha^-$.

The following theorem sets forth the principal result of this paper.

THEOREM 2.1. *Suppose that the equation*

$$a(t)-b(t)K(t)+c(t)K(t-\tau(t))=0$$

has a positive, ω-periodic, continuously differentiable solution $K(t)$. Then the model equation (2.1) *has a positive ω-periodic solution $Q(t)$. Moreover, if $b(t)>c(t)Q(t-\tau(t))/Q(t)$ for all $t\in[0,\omega]$, then $Q(t)$ is globally asymptotically stable with respect to positive solutions of* (2.1).

Remark 2.1. $K(t)$ represents the carrying capacity of the environment. If all of the growth rates a, b, and c are constant in time, then $K=a/b-c$. In the case where τ is also a constant, it is shown in [18] that the condition $b>c$ guarantees the global asymptotic stability of the carrying capacity. Our result here indicates that such a global asymptotic stability holds even when τ is not a constant.

Remark 2.2. In the case where $a(t)/(b(t)-c(t))$ is not a constant, the carrying capacity $K(t)$ must be an ω-periodic function, and the periodic solution $Q(t)$ obtained in our results is nonconstant.

Remark 2.3. In the case where $b(t)>c(t)$ for $t\in[0,\omega]$, by iterating the equation $K(t)=a(t)/b(t)+c(t)/b(t)K(t-\tau(t))$, we can get an explicit expression for $K(t)$

$$K(t)=\frac{a(t)}{b(t)}+\sum_{j=0}^{\infty}\prod_{i=0}^{j}\frac{c\circ m^i(t)}{b\circ m^i(t)}\frac{a\circ m^{j+1}(t)}{b\circ m^{j+1}(t)}, \tag{2.2}$$

where $m^0(t)=t$, $m^1(t)=t-\tau(t)$, $m^i(t)=m\circ m^{i-1}(t)$ for $t\in R$ and $i\geqq 1$. It is easy to see from the formula (2.2) that if $a(t)/b(t)-c(t)$ is not a constant, then the major role of the periodicity of the delay is to cause a periodic fluctuation of the corresponding carrying capacity about the carrying capacity which occurs when τ is a constant.

Remark 2.4. In applications, it is useful to have an estimate for the location of the periodic solution $Q(t)$. The proof of this theorem in the next section will provide a rough estimate of the constants ε and $M>0$ such that

$$\varepsilon\leqq\frac{Q(t)}{K(t)}\leqq M \quad \text{for } t\in[0,\omega].$$

This inequality also indicates that we can regard the periodic oscillation as being generated from the carrying capacity, in contrast to Cushing's result [14], where the periodic oscillation bifurcates from the trivial solution.

There is some experimental evidence [9] which indicates that continuously distributed delays are more realistic and more accurate than those with instantaneous time delays. Inspired by this evidence, we consider the following Volterra integro-differential equation

$$\dot{x}(t)=x(t)\left[a(t)-b(t)x(t)+\int_{-\infty}^{t}p(t,s)x(s)\,ds\right], \tag{2.3}$$

where $p(t,s)$ is a nonnegative continuous function satisfying $p(t+\omega,s+\omega)=p(t,s)$ for $-\infty<s\leqq t<+\infty$, and there exists a constant $\gamma>0$ such that

$$\int_{-\infty}^{0}p(t,t+\theta)\,e^{-\gamma\theta}\,d\theta<\infty \quad \text{for } t\in[0,\omega]. \tag{2.4}$$

The above assumptions are motivated and satisfied by the following special delay kernel

$$k(t,s)=\frac{1}{\tau^2(t)}\cdot(t-s)\cdot\exp\left[-\frac{1}{\tau(t)}(t-s)\right], \tag{2.5}$$

which attains its maximum at $s=t-\tau(t)$ for any fixed t. Therefore, (2.3) represents a continuously distributed delay analog of the difference-differential equation (2.1) with periodic discrete delay.

Let

$$C_\gamma=\left\{\varphi\in C((-\infty,0];R);\ \lim_{\theta\to-\infty}e^{\gamma\theta}\varphi(\theta)\text{ exists}\right\}$$

with

$$|\varphi|_{C_\gamma}=\sup_{-\infty<\theta\leqq 0}e^{\gamma\theta}|\varphi(\theta)|,\qquad \varphi\in C_\gamma,$$

and define $F:R\times C_\gamma\to R$ by

$$F(t,\varphi)=\varphi(0)\left[a(t)-b(t)\varphi(0)+\int_{-\infty}^{0}p(t,t+\theta)\varphi(\theta)\,d\theta\right],\qquad (t,\varphi)\in R\times C_\gamma.$$

Then $(C_\gamma, |\cdot|_{C_\gamma})$ is a Banach space which satisfies all of the fundamental axioms described in [26], and F is a continuous functional which is Lipschitz in $\varphi \in C_\gamma$. We notice that (2.3) can be reformulated as $\dot{x}(t) = F(t, x_t)$. Therefore, by Theorems 2.1-2.5 of [26], for each $\varphi \in C_\gamma$ there exists $\alpha := \alpha(\varphi) > 0$ and a unique solution $x(t; \varphi)$ of (2.3) defined on $(-\infty, \alpha)$ with $x_0 = \varphi$, and the mapping $(t, \varphi) \in (0, \alpha(\varphi)) \times C_\gamma \subseteq R \times C_\gamma \to x_t(\varphi) \in C_\gamma$ is continuous. Moreover, if $x(t; \varphi)$ is noncontinuable past $\alpha(\varphi)$ and $\alpha(\varphi) < \infty$, then $\lim_{t \to \alpha^-} |x(t; \varphi)| = \infty$.

The following result represents an analog of Theorem 2.1 in the case of distributed delay.

THEOREM 2.2. *Assume that there exists a continuously differentiable positive ω-periodic function $K(t)$ satisfying*

$$a(t) - b(t)K(t) + \int_{-\infty}^{t} p(t, s)K(s)\, ds = 0, \qquad t \in R;$$

then the model equation (2.3) *has a positive ω-periodic solution $Q(t)$. Moreover, if*

$$b(t) > \int_{-\infty}^{t} p(t, s) \frac{Q(s)}{Q(t)}\, ds, \qquad t \in R,$$

then $Q(t)$ is globally asymptotically stable with respect to positive solutions of (2.3) *in the state space C_γ.*

2.2. Nonlinear growth rates. In this part, we indicate a possible extension of our previous results to nonlinear growth rates. We consider the following model

$$\dot{x}(t) = x(t)[-D(t, x(t)) + B(t, x_t)], \tag{2.6}$$

where the death rate $D(t, x)$ is continuous in $(t, x) \in R^2$, ω-periodic in t, increasing and continuously differentiable in x; the birth rate $B(t, \varphi)$ is continuous in $(t, \varphi) \in R \times C([-\tau, 0]; R)$ (τ is a constant), continuously differentiable in $\varphi \in C([-\tau, 0]; R)$, and is ω-periodic in t in the following sense.

(H1) For any continuous ω-periodic function $x: R \to R$, $B(t, x_t)$ is ω-periodic as a function of t.

This model represents the case where there is a delay in the per capita birth rate, whereas the death rate is instantaneous [3], [5]. We assume that all positive feedbacks are included in the birth processes and any negative feedback is included in the death rate. Our crucial assumption is the following.

(H2) There exists a positive ω-periodic continuously differentiable function $K(t)$ such that $D(t, K(t)) = B(t, K_t)$ for $t \in R$.

With this assumption, Theorem 2.1 can be modified so as to apply to our nonlinear case.

THEOREM 2.3. *Suppose that*

(i) (H1)-(H2) *are satisfied.*

(ii) *For all $t \in [0, \omega]$, we have*

$$\inf_{x \in R^+} D_x(t, x) - \sup_{\varphi \in C} \|B_\varphi(t, \varphi)\| \cdot \frac{\max_{\theta \in [0,\omega]} K(\theta)}{K(t)} > 0, \tag{H3}$$

where $\|B_\varphi(t, \varphi)\|$ denotes the operator norm of the bounded linear operator $B_\varphi(t, \varphi)$: $C \to C$.

(iii) *There exists a constant $\delta > 0$ such that for every $\delta_0 \in (0, \delta)$, and for any $\varphi \in C$ with $\varphi(s) \geqq \varphi(0) = \delta_0$, we have $B(t, \varphi) - D(t, \varphi(0)) \geqq 0$.*

Then the model equation (2.6) *has a positive ω-periodic solution $Q(t)$. Moreover, if*

$$\inf_{x\in R^+} D_x(t,x) - \sup_{\varphi\in C} \|B_\varphi(t,\varphi)\| \frac{\max_{\theta\in[0,\omega]} Q(\theta)}{Q(t)} > 0$$

for all $t\in[0,\omega]$, then $Q(t)$ is globally asymptotically stable with respect to positive solutions of (2.6).

3. Proofs of theorems. In this section, we give detailed proofs for Theorems 2.1 and 2.2 and briefly indicate how to modify these proofs to the nonlinear case.

Let $C = C([-\tau^*, 0]; R)$ denote the Banach space of all continuous functions with the sup-norm

$$\|\varphi\| = \sup_{\theta\in[-\tau^*,0]} |\varphi(\theta)| \quad \text{for } \varphi\in C.$$

C^+ denotes a subset of C consisting of all nonnegative functions, $x(t;\varphi)$, $t\geqq -\tau^*$, $\varphi\in C^+$, denotes the unique solution of equation (2.1) satisfying $x(t;\varphi)=\varphi(t)$ on $[-\tau^*, 0]$, and $x_t(\varphi)\in C$ is defined as $x_t(\varphi)(s) = x(t+s;\varphi)$ for all $s\in[-\tau^*,0]$.

LEMMA 3.1. *There exists a constant $\delta>0$ such that for every $\delta_0\in(0,\delta)$, the set*

$$B^C_{\delta_0} = \{\varphi\in C^+ : \varphi(\theta)\geqq\delta_0 \quad \textit{for } \theta\in[-\tau^*,0]\}$$

is invariant, that is, $\varphi\in B^C_{\delta_0}$ implies $x_t(\varphi)\in B^C_{\delta_0}$ for all $t\geqq 0$.

Proof. We select a constant $\delta>0$ such that

$$\inf_{t\in[0,\omega]} \{a(t) - b(t)\delta\} > 0.$$

Let $\delta_0\in(0,\delta)$ and $\varphi\in B^C_{\delta_0}$ be given. We consider the solution $x(t) = x(t;\varphi)$ of (2.1). If at an instant $t\geqq 0$ we have $x^2(s)\geqq x^2(t) = \delta_0^2$ for $s\in[t-\tau^*, t]$, then $[x^2(t)]'\leqq 0$. However, from (2.1) we have

$$\begin{aligned}[x^2(t)]' &= 2x^2(t)[a(t) - b(t)x(t) + c(t)x(t-\tau(t))]\\ &\geqq 2x^2(t)[a(t) - b(t)\delta_0]\\ &> 0.\end{aligned}$$

This contradiction indicates that $\min\{\min_{\theta\in[-\tau^*,0]} x^2(t+\theta), \delta_0^2\}$ is nondecreasing, and therefore

$$\min\left\{\min_{\theta\in[-\tau^*,0]} x^2(t+\theta), \delta_0^2\right\} \geqq \min\left\{\min_{\theta\in[-\tau^*,0]} \varphi^2(\theta), \delta_0^2\right\} = \delta_0^2$$

for all $t\geqq 0$. This completes the proof.

LEMMA 3.2. *For any $\rho>1$, we have*

$$\rho x - \ln(\rho x) \geqq \beta[x - \ln x] \quad \textit{for all } x\geqq 1$$

where $\beta = \rho - \ln\rho$.

Proof. Let $G(x) = \rho\ln x - \ln(\rho x) + (1/x)\ln\rho$. Then $G(1) = 0$, $G(\infty)=\infty$, and

$$G'(x) = \frac{1}{x^2}[(\rho-1)x - \ln\rho]$$

from which we know that $G'(x)>0$ for $x>\ln\rho/(\rho-1)$ and $G'(x)<0$ for $x<\ln\rho/(\rho-1)$. Therefore there exists a unique $x^*>1$ such that $G(x^*)=\rho-1$, $G(x)>1$ if $x>x^*$ and $G(x)<\rho-1$ for $x<x^*$.

Consider now $f(x)=(\rho x-\ln(\rho x))/(x-\ln x)$. Then

$$f'(x)=\frac{\rho-1-\rho\ln x+\ln(\rho x)-(\ln\rho)/x}{(x-\ln x)^2}$$

$$=\frac{\rho-1-G(x)}{(x-\ln x)^2}$$

which implies that $f'(x)>0$ if $x<x^*$, and $f'(x)<0$ if $x>x^*$. Therefore

$$f(x)\geqq\min\{f(1),f(\infty)\}=\min\{\rho-\ln\rho,\rho\}=\rho-\ln\rho$$

for all $x\geqq 1$. This completes the proof.

The following result describes a dissipative property of the equation, where the existence of an attracting region is essential for our main results.

LEMMA 3.3. *Assume that*

$$\frac{c(t)}{K(t)}K(t-\tau(t))<b(t)\quad \text{on } [0,\omega].$$

Then

(i) *For any* $\xi\geqq\delta$, *there exists a constant* $d:=d(\xi)>0$ *such that for any* $\varphi\in C$ *with* $\delta\leqq\varphi(\theta)\leqq\xi$ *on* $[-\tau^*,0]$, *we have* $\delta\leqq x(t;\varphi)\leqq d(\xi)$ *for all* $t\geqq 0$;

(ii) *There exists a constant* $M\geqq\delta$ *such that for any* $\beta\geqq\delta$ *there is a constant* $T=T(\beta)>0$ *such that for any* $\varphi\in C$ *with* $\delta\leqq\varphi(\theta)\leqq\beta$ *on* $[-\tau^*,0]$ *we have* $\delta\leqq x(t;\varphi)\leqq M$ *for all* $t\geqq T(\beta)$.

Proof. According to the assumptions, we can find a constant $\rho>1$ such that

$$\min_{t\in[0,\omega]}\left\{b(t)-\rho\cdot\frac{c(t)}{K(t)}\cdot K(t-\tau(t))\right\}=\delta_1>0.$$

For such $\gamma>1$, define

$$M^*=\frac{2}{\delta_1}\max_{0\leqq t\leqq\omega}\left\{(\rho-1)c(t)\max_{\theta\in[0,\omega]}K(\theta)+\frac{|\dot K(t)|}{K(t)}\right\}+\max_{\theta\in[0,\omega]}K(\theta).$$

Define a continuous map $V:R\times(0,\infty)\to R$ by

$$V(t,x)=\frac{x}{K(t)}-\ln\frac{x}{K(t)}\quad\text{for } (t,x)\in R\times(0,\infty).$$

Suppose $x(t)=x(t;\varphi)$ is a solution of (2.1) with $\min_{\theta\in[-\tau^*,0]}\varphi(\theta)\geqq\delta$. By Lemma 3.1, $x(t)\geqq\delta$ for all $t\geqq 0$, and therefore $V(t,x(t))$ is well defined and differentiable for $t\geqq 0$. Moreover, we have

$$\frac{d}{dt}V(t,x(t))=\left[1-\frac{K(t)}{x(t)}\right]\left\{\frac{x(t)}{K(t)}[a(t)-b(t)x(t)+c(t)x(t-\tau(t))]-\frac{\dot K(t)}{K^2(t)}x(t)\right\}$$

$$=\frac{x(t)-K(t)}{K(t)}\left\{a(t)-b(t)x(t)+c(t)x(t-\tau(t))-\frac{\dot K(t)}{K(t)}\right\}$$

$$=-\frac{x(t)-K(t)}{K(t)}\left\{b(t)[x(t)-K(t)]\right.$$

$$\left.-c(t)[x(t-\tau(t))-K(t-\tau(t))]-\frac{\dot K(t)}{K(t)}\right\}.$$

Suppose at some $t \geqq 0$, we have

$$V(t+s, x(t+s)) \leqq (\rho - \ln \rho) V(t, x(t)) \quad \text{for } s \in [-\tau^*, 0]$$

and $x(t) \geqq M^*$. Then by Lemma 3.2, we have

$$\frac{x(t+s)}{K(t+s)} - \ln \frac{x(t+s)}{K(t+s)} \leqq \frac{\rho x(t)}{K(t)} - \ln \left(\frac{\rho x(t)}{K(t)} \right)$$

for all $s \in [-\tau^*, 0]$. From the choice of M^*, it follows that

$$\frac{x(t)}{K(t)} \geqq \frac{M^*}{K(t)} \geqq 1,$$

and therefore by the increasing property of the function $u - \ln u$ for $u \geqq 1$, we get

$$\frac{x(t+s)}{K(t+s)} \leqq \frac{\rho x(t)}{K(t)} \quad \text{for } s \in [-\tau^*, 0].$$

Hence

$$x(t+s) - K(t+s) \leqq \frac{K(t+s)}{K(t)} \rho[x(t) - K(t)] + (\rho - 1) K(t+s)$$

for all $s \in [-\tau^*, 0]$. This implies that

$$\begin{aligned}
-K(t) \frac{d}{dt} V(t, x(t)) &= b(t)[x(t) - K(t)]^2 - c(t)[x(t) - K(t)][x(t - \tau(t)) - K(t - \tau(t))] \\
&\quad - \frac{\dot{K}(t)}{K(t)} [x(t) - K(t)] \\
&\geqq b(t)[x(t) - K(t)]^2 - c(t) \cdot \frac{K(t - \tau(t))}{K(t)} [x(t) - K(t)]^2 \rho \\
&\quad - (\rho - 1) c(t) K(t - \tau(t)) |x(t) - K(t)| - \frac{\dot{K}(t)}{K(t)} [x(t) - K(t)] \\
&\geqq \left[b(t) - \rho \frac{c(t)}{K(t)} \cdot K(t - \tau(t)) \right] [x(t) - K(t)]^2 \\
&\quad - \left[(\rho - 1) c(t) \max_{\theta \in [0, \omega]} K(\theta) + \frac{|\dot{K}(t)|}{K(t)} \right] |x(t) - K(t)| \\
&\geqq \delta_1 [x(t) - K(t)]^2 \\
&\quad - \left[(\rho - 1) c(t) \max_{\theta \in [0, \omega]} K(\theta) + \frac{|\dot{K}(t)|}{K(t)} \right] |x(t) - K(t)| \\
&\geqq \frac{1}{2} \delta_1 |x(t) - K(t)|^2.
\end{aligned}$$

That is,

$$\frac{d}{dt} V(t, x(t)) \leqq - \frac{\delta_1}{2 \max_{\theta \in [0, \omega]} K(\theta)} |x(t) - K(t)|^2$$

whenever $V(t+s, x(t+s)) \leqq (\gamma - \ln \gamma) V(t, x(t))$ for $s \in [-\tau^*, 0]$ and $x(t) \geqq M^*$. Therefore, employing a variation of the standard argument of the uniform boundedness and uniform ultimate boundedness theorem of Lyapunov-Razumikhim type [25], we can prove the conclusion with any given constant $M > M^*$.

The following result from [27] is our major tool used in guaranteeing the existence of a ω-periodic solution.

LEMMA 3.4 (Horn's fixed-point theorem). *Let $S_0 \subset S_1 \subset S_2$ be convex subsets of the Banach space X, with S_0 and S_2 compact and S_1 open relative to S_2. Let $P: S_2 \to X$ be a continuous mapping such that, for some integer $m > 0$,*

(a) $P^j(S_1) \subseteq S_2$, $1 \leqq j \leqq m-1$,

and

(b) $P^j(S_1) \subseteq S_0$, $m \leqq j \leqq 2m-1$.

Then P has a fixed point in S_0.

Now we are in a position to prove our major results.

Proof of Theorem 2.1. Let $M \geqq \delta$ be given according to (ii) of Lemma 3.3. By (i) of Lemma 3.3, we can find a constant $M_1 > M+1$ such that $\delta \leqq \varphi(\theta) \leqq M+1$ on $[-\tau^*, 0]$ implies $\delta \leqq x(t; \varphi) \leqq M_1$ for all $t \geqq 0$. By (ii) of Lemma 3.3, we can find a constant $T_1 > 0$ such that $\delta \leqq \varphi(\theta) \leqq M_1 + 1$ on $[-\tau^*, 0]$ implies $\delta \leqq x(t; \varphi) \leqq M$ for all $t \geqq T_1$. Similarly, we can find constants M_2 and $M_3 > \delta$ such that

$$\delta \leqq \varphi(\theta) \leqq M_1 + 1 \quad \text{on } [-\tau^*, 0] \quad \text{implies } \delta \leqq x(t; \varphi) \leqq M_2$$

for all $t \geqq 0$, *and*

$$\delta \leqq \varphi(\theta) \leqq M_2 \quad \text{on } [-\tau^*, 0] \quad \text{implies } \delta \leqq x(t; \varphi) \leqq M_3$$

for all $t \geqq 0$.

Define

$$L = M_3 \sup_{t \in [0, \omega]} \{a(t) + b(t)M_3 + c(t)M_3\}$$

and

$$S_0 = \{\varphi \in C; \delta \leqq \varphi(\theta) \leqq M+1, |\varphi(\theta) - \varphi(\eta)| \leqq L|\theta - \eta| \quad \text{for } \theta, \eta \in [-\tau^*, 0]\},$$

$$S_1 = \{\varphi \in C; \delta \leqq \varphi(\theta) < M_1+1, |\varphi(\theta) - \varphi(\eta)| \leqq L|\theta - \eta| \quad \text{for } \theta, \eta \in [-\tau^*, 0]\},$$

$$S_2 = \{\varphi \in C; \delta \leqq \varphi(\theta) \leqq M_2, |\varphi(\theta) - \varphi(\eta)| \leqq L|\theta - \eta| \quad \text{for } \theta, \eta \in [-\tau^*, 0]\}.$$

As well, define a Poincaré map $P: S_2 \to C$ by

$$P(\varphi) = x_\omega(\varphi) \quad \text{for } \varphi \in S_2.$$

Then by the uniqueness and continuous dependence of solutions and the periodicity of a, b, c and τ, we have $P^n(\varphi) = x_{n\omega}(\varphi)$ for all integers $n \geqq 0$, and furthermore P is a continuous map. Evidently, $S_0 \subset S_1 \subset S_2$ are convex subsets of the Banach space C, with S_0 and S_2 compact (Arzola–Ascoli's theorem) and S_1 open relative to S_2. Choose an integer $m > 0$ such that $m\omega > T_1$. Then

$$P^j(S_1) \subseteq S_2 \quad \text{for all } j \geqq 1$$

and

$$P^j(S_1) \subseteq S_0 \quad \text{for all } j \geqq m.$$

Now by Horn's asymptotic fixed point theorem, P has a fixed point in S_0. That is, there is a ω-periodic solution $Q(t)$ of (2.1) with $Q(t) \geqq \delta$ for $t \in [0, \omega]$.

To prove the global asymptotic stability of $Q(t)$ with respect to positive solutions of (2.1), we note that

$$\left[\ln \frac{x(t)}{Q(t)}\right]' = -b(t)[x(t) - Q(t)] + c(t)[x(t-\tau(t)) - Q(t-\tau(t))].$$

Let $u(t)=x(t)-Q(t)$. We get

$$\left[\ln\left(1+\frac{u(t)}{Q(t)}\right)\right]'=-b(t)u(t)+c(t)u(t-\tau(t)).$$

The change of variable

$$\ln\left(1+\frac{u(t)}{Q(t)}\right)=y(t)$$

or equivalently,

$$u(t)=[e^{y(t)}-1]Q(t)$$

leads to the equation

$$\dot{y}(t)=-b(t)Q(t)[e^{y(t)}-1]+c(t)Q(t-\tau(t))[e^{y(t-\tau(t))}-1]. \tag{3.5}$$

Consider the function $W(t)=[e^{y(t)}-1]^2$ and choose a constant $\rho^*>1$ such that

$$\rho^*c(t)Q(t-\tau(t))<b(t)Q(t) \quad \text{for } t\in[0,\omega].$$

If at an instant $t\geqq 0$, we have

$$W(y(s))\leqq\rho^*W(y(t)) \quad \text{for all } s\in[t-\tau(t),t],$$

then

$$\begin{aligned}\frac{d}{dt}W(y(t))&=-2\,e^{y(t)}\{b(t)Q(t)[e^{y(t)}-1]^2-c(t)Q(t-\tau(t))[e^{y(t-\tau(t))}-1][e^{y(t)}-1]\}\\&\leqq-2\,e^{y(t)}\{b(t)Q(t)[e^{y(t)}-1]^2-\rho^*c(t)Q(t-\tau(t))[e^{y(t)}-1]^2\}\\&\leqq-2\varepsilon\,e^{y(t)}[e^{y(t)}-1]^2,\end{aligned}$$

where $\varepsilon=\inf_{t\in[0,\omega]}\{b(t)Q(t)-\rho^*c(t)Q(t-\tau(t))\}>0$. Therefore, by the uniform asymptotic stability theorem of Lyapunov-Razumikhin type, we are assured that the zero solution of (3.5) is globally uniformly asymptotically stable, that is, the ω-periodic solution $Q(t)$ of (2.1) is uniformly globally asymptotically stable with respect to positive solutions of (2.1). The proof is completed.

Proof of Theorem 2.2. First of all, using an argument similar to that for Lemma 3.1, we can show that if $\delta>0$ is sufficiently small, so that $a(t)-b(t)\delta>0$ for $t\in[0,\omega]$, then for any $\varphi\in C_\gamma$ with $\varphi(\theta)\geqq\delta$ for $\theta\leqq 0$, we have $x(t;\varphi)\geqq\delta$ for $t\geqq 0$.

Let $BC_\gamma=\{\varphi\in C_\gamma;\ \sup_{\theta\leqq 0}|\varphi(\theta)|<\infty\}$. We next prove that for any $\xi\geqq\delta$ there exists $d(\xi)>0$ such that if $\varphi\in BC_\gamma$ is given, so that $\delta\leqq\varphi(\theta)\leqq\xi e^{-\gamma\theta}$ for $\theta\leqq 0$, then $\delta\leqq x(t;\varphi)\leqq d(\varphi)$ for $t\geqq 0$. In fact, for the function $V:R\times(0,\infty)\to R$ defined by $V(t,x)=(x/K(t))-\ln(x/K(t))$, and for $x(t):=x(t;\varphi)$, we have

$$\frac{d}{dt}V(t,x(t))=-\frac{x(t)-K(t)}{K(t)}\cdot\left\{b(t)[x(t)-K(t)]-\int_{-\infty}^{t}p(t,s)[x(s)-K(s)]\,ds-\frac{\dot{K}(t)}{K(t)}\right\}.$$

Since $u-\ln u$ is an increasing and unbounded function for $u\geqq 1$, we can find a constant $N_1\geqq\max_{\delta\leqq\varphi(0)\leqq\xi}V(0,\varphi(0))$ such that if $\max\{N_1,V(s,x(s))\}\leqq V(t,x(t))$ for $s\leqq t$, then $\max\{N_2, x(s)/K(s)\} \leqq x(t)/K(t)$ for $s \leqq t$, where

$$N_2 = \max_{t\in[0,\omega]} \frac{|\dot K(t)|/K(t)}{b(t) - \int_{-\infty}^{t} p(t,s)[K(s)/K(t)]\,ds}.$$

Therefore, if $\max\{N_1, V(s, x(s))\} \leqq V(t, x(t))$ for $s \leqq t$, then $x(s) - K(s) \leqq (K(s)/K(t))[x(t) - K(t)]$ for $s \leqq t$, and

$$\begin{aligned}\frac{d}{dt} & V(t, K(t)) \\ &\leqq -\frac{1}{K(t)}\left\{\left[b(t) - \int_{-\infty}^{t} p(t,s)\frac{K(s)}{K(t)}\,ds\right][x(t)-K(t)]^2 - \frac{|\dot K(t)|}{K(t)}|x(t)-K(t)|\right\} \\ &\leqq 0.\end{aligned}$$

Therefore, $V(t, x(t)) \leqq N_1$ for $t \geqq 0$, which implies the existence of $d(\xi)$.

We then show that there exists a constant $M \geqq \delta$ such that for any $\xi \geqq \delta$ there is a constant $T(\xi) > 0$ such that if $\varphi \in BC_\gamma$ and $\delta \leqq \varphi(\theta) \leqq \xi e^{-\gamma\theta}$ for $\theta \leqq 0$, then $\delta \leqq x(t; \varphi) \leqq M$ for all $t \geqq T(\xi)$. In fact, from the condition (2.4), for any $\varphi \geqq \delta$, we can choose $q(\xi) > 0$ such that

$$\int_{-\infty}^{-q(\xi)} p(t, t+\theta)\, e^{-\gamma\theta}\, d\theta \leqq \frac{1}{\xi + d(\varphi) + |K_0|_\gamma + \max_{0\leqq s\leqq\omega} K(s)}, \quad t \in [0, \omega].$$

Therefore,

$$\begin{aligned}\int_{-\infty}^{-q(\xi)} & p(t, t+\theta)|x(t+\theta) - K(t+\theta)|\, d\theta \\ &\leqq \int_{-\infty}^{-q(\xi)} p(t, t+\theta)\, e^{-\gamma\theta}\, d\theta \left[\sup_{s\leqq -t} |x(t+s) - K(t+s)|\, e^{\gamma(t+s)}\, e^{-\gamma t}\right. \\ &\qquad\qquad \left. + \sup_{-t\leqq s\leqq 0} |x(t+s) - K(t+s)|\right] \\ &\leqq \int_{-\infty}^{-q(\xi)} p(t, t+\theta)\, e^{-\gamma\theta}\, d\theta \left[\xi + |K_0|_{C_\gamma} + d(\xi) + \max_{0\leqq s\leqq\omega} K(s)\right] \\ &\leqq 1.\end{aligned}$$

We now find a constant $\rho > 1$ such that

$$\min_{t\in[0,\omega]} \left\{b(t) - \rho \int_{-\infty}^{t} p(t,s)\frac{K(s)}{K(t)}\,ds\right\} = \delta_1 > 0$$

and define

$$M^* = \frac{2}{\delta_1}\left[1 + (\rho - 1)\sup_{0\leqq t\leqq\omega}\left\{\int_{-\infty}^{t} p(t,s)K(s)\,ds + \frac{|\dot K(t)|}{K(t)}\right\}\right].$$

Then using an argument similar to that for Lemma 3.3, we can see that if at some $t \geqq 0$, $V(s, x(s)) \leqq (\rho - \ln\rho) V(t, x(t))$ for $s \in [t - q(\xi), t]$ and $x(t) \geqq M^*$, then

$$x(s) - K(s) \leqq \frac{K(s)}{K(t)}\rho[x(t) - K(t)] + (\rho - 1)K(s)$$

for $s \in [t-q(\xi), t]$, and hence

$$-K(t)\frac{d}{dt}V(t,x(t)) \geqq b(t)[x(t)-K(t)]^2 - \int_{-\infty}^{t-q(\xi)} p(t,s)[x(s)-K(s)]\,ds|x(t)-K(t)|$$
$$-\int_{t-q(\xi)}^{t} p(t,s)\frac{K(s)}{K(t)}\rho[x(t)-K(t)]^2\,ds$$
$$-\int_{t-q(\xi)}^{t} p(t,s)(\rho-1)K(s)|x(t)-K(t)|\,ds$$
$$-\frac{|\dot K(t)|}{K(t)}|x(t)-K(t)|$$
$$\geqq \frac{\delta_1}{2}|x(t)-K(t)|^2.$$

Therefore, employing a variation of the standard argument of the uniform ultimate boundedness theorem of Lyapunov-Razumikhin type [25], we can prove the existence of M.

The rest of the proof is similar to the proofs for Theorem 2.1 and Theorem 3.1 of [1], and therefore is omitted.

Proof of Theorem 2.3. We construct a Lyapunov function $V(t,x) = (x/K(t)) - \ln(x/K(t))$ for $(t,x) \in R \times (0,\infty)$, and select a constant $\rho > 0$ such that

$$\inf_{x\in R^+} D_x(t,x) - \rho \sup_{\varphi\in C} \|B_\varphi(t,\varphi)\| \frac{\max_{\theta\in[0,\omega]} K(\theta)}{K(t)} \geqq \delta_1 > 0,$$

where $\delta_1 > 0$ is a constant. It is easy to obtain

$$\frac{d}{dt}V(t,x(t)) = -\frac{x(t)-K(t)}{K(t)}[D(t,x(t))-B(t,x_t)] - \frac{x(t)-K(t)}{K^2(t)}\dot K(t)$$
$$= -\frac{x(t)-K(t)}{K(t)}[D(t,x(t))-D(t,K(t))]$$
$$+\frac{x(t)-K(t)}{K(t)}[B(t,x_t)-B(t,K_t)] - \frac{x(t)-K(t)}{K^2(t)}\dot K(t)$$
$$\leqq -\frac{[x(t)-K(t)]^2}{K(t)} \inf_{x\in R^+} D_x(t,x)$$
$$+\sup_{\varphi\in C}\|B_\varphi(t,\varphi)\| \frac{|x(t)-K(t)|}{K(t)}\|x_t-K_t\| - \frac{x(t)-K(t)}{K^2(t)}\dot K(t).$$

Therefore, if

$$V(t+s, x(t+s)) \leqq (\rho - \ln\rho)V(t,x(t)) \quad \text{for } s\in[-\tau^*, 0]$$

and

$$x(t) \geqq M^* = \frac{2}{\delta_1}\sup_{t\in[0,\omega]}\left\{(\rho-1)\sup_{\varphi\in C}\|B_\varphi(t,\varphi)\| \max_{\varphi\in[0,\omega]} K(\theta) + \frac{|\dot K(t)|}{K(t)}\right\}$$
$$+\max_{\theta\in[0,\omega]} K(\theta).$$

Then by Lemma 3.2, we can obtain

$$\frac{dV(t,x(t))}{dt} \leqq -\frac{\delta_1}{2\max_{\theta\in[0,\omega]}K(\theta)}|x(t)-K(t)|^2.$$

Hence results in Lemma 3.3 are valid. The rest of the proof is exactly the same as that for Theorem 2.1 and therefore is omitted.

Discussion. In this paper we have considered several single-species models with time delays where both the coefficients and the delays are periodic functions. These models are based on laboratory evidence in observing the population growth of rotifers.

The model given by (2.1) is of retarded type, whereas the model described by (2.3) incorporates a distributed periodic delay. However, both of these are of Lotka–Volterra type. It would be of interest to consider equations of single-species which are more general. Unfortunately, we are not able to do so at this time, since some of the technical steps in our method of proofs of the existence of positive periodic solutions require the Lotka–Volterra format.

It would also be of interest to consider higher-dimensional systems with periodic delays, representing predator-prey or competitive systems. Again, this is likely to be considerably more difficult, and we leave this for future work.

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