数理解析研究所講究録 1372 巻 2004 年 7-16

A delay model for inverse trophic relationship

齋藤 保久[†] 竹内 康博[*]
(Yasuhisa Saito) (Yasuhiro Takeuchi)
静岡大学工学部
(Department of Systems Engineering, Shizuoka University)

1. Introduction

A fair amount of previous work have been appeared on modeling stage-structured population growth consisting of immature and mature individuals for species (see [1, 2, 8, 10, 11] and the references cited therein). In most of the studies, stage-structure is modeled by the introduction of a time delay, which leads to systems of retarded functional differential equations. [1] proposed a model of single species growth incorporating stage-structure as a reasonable generalization of the logistic model, which takes the form

$$\begin{aligned} y'(t) &= -\gamma y(t) + \alpha Y(t) - \alpha e^{-\gamma\tau} Y(t-\tau), \\ Y'(t) &= -\beta Y^2(t) + \alpha e^{-\gamma\tau} Y(t-\tau). \end{aligned} \tag{1}$$

Here, y and Y denote the densities of immature and mature populations for single species, respectively, where τ represents a constant time to maturity. $\gamma > 0$ is the death rate in immature stage and $\alpha > 0$ denotes the birth rate of the species. $\beta > 0$ is the mature death that reflects overcrowding effect. The term $\alpha e^{-\gamma\tau} Y(t-\tau)$ of the first expression of (1) represents the immatures born at time $t-\tau$ (with the mature birth rate α) that survive to time t (with the immature death rate γ). This suggests that those immatures exit from the immature population and enter the mature population at time t. For (1), it is known that there exists a unique global asymptotic stable interior equilibrium for solutions with the initial condition $y(0) > 0$ and $Y(t) > 0$ on $-\tau \le t \le 0$ (see [1, Theorem 2]).

In the real world, it is often observed that, for example, predatory plankton eaten by mature fish is predatory to the immature — which is called *inverse trophic relationship*

[†]The research was partly supported by the Ministry of Education, Culture, Sports, Science and Technology in Japan, under Grand-in-Aid for JSPS Fellows 00000472.

[*]The research was partly supported by the Ministry of Education, Culture, Sports, Science and Technology in Japan, under Grand-in-Aid for Scientific Research(A) 13304006.

(see, for example [3, 4, 6, 7]). The authors, in [9], considered a stage-structured prey-predator model based on (1) as follows:

$$
\begin{aligned}
x'(t) &= x(t)[r_1 - a_{11}x(t) - a_{13}Y(t)],\\
y'(t) &= -r_2 y(t) + a_{31}x(t)Y(t) - a_{31}e^{-r_2\tau}x(t-\tau)Y(t-\tau),\\
Y'(t) &= -r_3 Y^2(t) + a_{31}e^{-r_2\tau}x(t-\tau)Y(t-\tau).
\end{aligned}
\tag{2}
$$

Here, x is the density of prey, and y and Y denote the densities of the immature and mature predator populations, respectively, where τ represents a constant time to maturity for predator. [9] has been established sufficient conditions for the local asymptotic stability and global attractivity of an interior equilibrium of the model. In this paper, to discuss the effect of inverse trophic relationship on population dynamics, we propose a time-delay model for "prey counterattack" against predator, based on the model (2). We believe that this is the first time such a population model has appeared in the literature.

In the next section, we present our model and results. The proof of our theorems are given in Sections 3 and 4. In the final section, we give some discussion and future work.

2. The Model and Main Results

We propose the following time-delay model for inverse trophic relationship:

$$
\begin{aligned}
x'(t) &= x(t)[r_1 - a_{11}x(t) + \alpha_1 y(t) - a_{13}Y(t)]\\
y'(t) &= [-r_2 - \alpha_2 x(t)]y(t) + a_{31}x(t)Y(t)\\
&\qquad - a_{31}x(t-\tau)Y(t-\tau)e^{\int_{t-\tau}^{t}[-r_2-\alpha_2 x(s)]ds}\\
Y'(t) &= -r_3 Y^2(t) + a_{31}x(t-\tau)Y(t-\tau)e^{\int_{t-\tau}^{t}[-r_2-\alpha_2 x(s)]ds},
\end{aligned}
\tag{3}
$$

where α_1 and α_2 are nonnegative constants that reflect inverse trophic relationship, and all the rest of parameters are positive. x is the prey of Y but eats y, which we may also call *prey counterattack with time delay.* We assume that the growth rate of x is of a Lotka-Volterra nature, and that the mature predator population cannot give birth to immatures without prey x (i.e. $a_{31}x(t)Y(t)$ and $a_{31}e^{-r_2\tau}x(t-\tau)Y(t-\tau)$).

The initial condition of (3) is given as $x(s) \geq 0$ and $Y(s) \geq 0$ on $-\tau \leq s \leq 0$, and $x(0) > 0$, $y(0) > 0$, and $Y(0) > 0$. For (3), it is straightforward to see that there exist two boundary equilibria $(0,0,0)$ and $(\frac{r_1}{a_{11}}, 0, 0)$ which are always unstable. However, one cannot immediately see the existence, uniqueness, and stability of an interior equilibrium for (3). In fact, let (x^*, y^*, Y^*) be possible interior equilibria of (3). Then, they satisfy

$$
\begin{aligned}
&r_1 - a_{11}x^* + \alpha_1 y^* - a_{13}Y^* = 0,\\
&(-r_2 - \alpha_2 x^*)y^* + a_{31}x^*Y^*\left(1 - e^{(-r_2-\alpha_2 x^*)\tau}\right) = 0,\\
&-r_3 Y^* + a_{31}x^* e^{(-r_2-\alpha_2 x^*)\tau} = 0.
\end{aligned}
$$

One cannot solve (x^*, y^*, Y^*) in any explicit forms of parameters since the third expression has transcendental relationship between x^* and Y^*.

When there is no inverse trophic relationship, that is, $\alpha_1 = \alpha_2 = 0$, the model (3) is reduced to (2). In this case, the system has a unique interior equilibrium expressed in an explicit form of parameters and qualitative properties that (i) *all solutions of (3) tend to the interior equilibrium as* $t \to +\infty$ *if* $a_{11}r_3 > a_{13}a_{31}e^{-r_2\tau}$; (ii) *the interior equilibrium is locally asymptotically stable for all* $\tau > 0$ *if* $3a_{11}r_3 \geq a_{13}a_{31}$ (see [9]). In order to clarify the effect of inverse trophic relationship, it may be natural to think that we should discuss qualitative properties for inverse trophic relationship under those conditions which ensure global attractivity or local asymptotic stability for the system with $\alpha_1 = \alpha_2 = 0$.

Our final goal is to find some global bifurcation caused by the effect of inverse trophic relationship for (3). In this paper, we consider the case when $\alpha_1 = 0$ and $\alpha_2 > 0$, which is unrealistic from a biological point of view but may be a first step to reaching the goal. We have the following two theorems, which show that the case $\alpha_1 = 0$ and $\alpha_2 > 0$ has completely the same global properties as $\alpha_1 = \alpha_2 = 0$:

Theorem 1. *Suppose* $\alpha_1 = 0$. *Then, system (3) has a unique interior equilibrium to which all the solutions tend as* $t \to +\infty$ *if* $a_{11}r_3 > a_{13}a_{31}e^{-r_2\tau}$ *holds.*

Theorem 2. *Suppose* $\alpha_1 = 0$ *and that* τ_0 *is a positive value determined by* $a_{11}r_3 = a_{13}a_{31}e^{-r_2\tau_0}$. *Then, the interior equilibrium of (3) is globally asymptotically stable for all* $\tau > \tau_0$ *if* $3a_{11}r_3 \geq a_{13}a_{31}$ *holds.*

3. Global Attractivity of an Interior Equilibrium

In this section, we will prove Theorem 1.

Proof. We first focus on the system of the first and third expressions of (3);

$$\begin{aligned} x'(t) &= x(t)[r_1 - a_{11}x(t) - a_{13}Y(t)], \\ Y'(t) &= -r_3Y^2(t) + a_{31}x(t-\tau)Y(t-\tau)e^{\int_{t-\tau}^{t}[-r_2-\alpha_2 x(s)]ds}. \end{aligned} \tag{4}$$

From the first expression of (4) we have $x'(t) \leq x(t)[r_1 - a_{11}x(t)]$ for $t \geq 0$. By comparison, for any sufficiently small $\varepsilon_1^x > 0$,

$$x(t) \leq \frac{r_1}{a_{11}} + \varepsilon_1^x$$

holds for all large $t > 0$. We then have from the second expression of (4) that for all large $t > 0$,

$$Y'(t) \leq -r_3Y^2(t) + a_{31}M_1^x e^{-r_2\tau}Y(t-\tau), \tag{5}$$

where $M_1^x = \frac{r_1}{a_{11}} + \varepsilon_1^x$. Now consider the scalar delay differential equation

$$z'(t) = -r_3z^2(t) + a_{31}M_1^x e^{-r_2\tau}z(t-\tau).$$

It is known that all solutions $z(t)$ of the equation tend to $\frac{a_{31}e^{-r_2\tau}M_1^x}{r_3}$ as $t \to +\infty$ (see [1]). Therefore, by comparison and (5), for any sufficiently small $\varepsilon_1^Y > 0$,

$$Y(t) \le \frac{a_{31}M_1^x e^{-r_2\tau}}{r_3} + \varepsilon_1^Y$$

holds for all large t.

Let $M_1^Y = \frac{a_{31}M_1^x e^{-r_2\tau}}{r_3} + \varepsilon_1^Y$. Then, from (4) we have for all large t,

$$x'(t) \ge x(t)\left[r_1 - a_{13}M_1^Y - a_{11}x(t)\right].$$

Here, one can make $r_1 - a_{13}M_1^Y$ positive by choosing ε_1^x and ε_1^Y such that

$$0 < \varepsilon_1^x < \frac{r_1(a_{11}r_3 - a_{13}a_{31}e^{-r_2\tau})}{a_{11}a_{13}a_{31}e^{-r_2\tau}},$$
$$0 < \varepsilon_1^Y < \frac{r_1(a_{11}r_3 - a_{13}a_{31}e^{-r_2\tau}) - a_{11}a_{13}a_{31}e^{-r_2\tau}\varepsilon_1^x}{a_{11}a_{13}r_3}$$

since $a_{11}r_3 > a_{13}a_{31}e^{-r_2\tau}$. By comparison, there exists sufficiently small $\delta_1^x > 0$ such that

$$x(t) \ge \frac{r_1 - a_{13}M_1^Y}{a_{11}} - \delta_1^x > 0$$

for all large t. We then have from (4) that for all large t,

$$Y'(t) \ge -r_3Y^2(t) + a_{31}L_1^x e^{\tau(-r_2-\alpha_2 M_1^x)}Y(t-\tau),$$

where $L_1^x = \frac{r_1 - a_{13}M_1^Y}{a_{11}} - \delta_1^x$. Similarly, comparison implies that there exists sufficiently small $\delta_1^Y > 0$ such that for all large t,

$$Y(t) \ge \frac{a_{31}L_1^x e^{\tau(-r_2-\alpha_2 M_1^x)}}{r_3} - \delta_1^Y > 0.$$

Let $L_1^Y = \frac{a_{31}L_1^x e^{\tau(-r_2-\alpha_2 M_1^x)}}{r_3} - \delta_1^Y$. Hence, for all large t, all solutions $(x(t), Y(t))$ satisfy

$$L_1^x \le x(t) \le M_1^x,$$
$$L_1^Y \le Y(t) \le M_1^Y.$$

From (4) again, for all large t,

$$x'(t) \le x(t)\left[r_1 - a_{13}L_1^Y - a_{11}x(t)\right]$$

holds, which implies that there exists sufficiently small ε_2^x; $\varepsilon_1^x > \varepsilon_2^x > 0$ such that

$$x(t) \le \frac{r_1 - a_{13}L_1^Y}{a_{11}} + \varepsilon_2^x$$

for all large t. Then, from (4) we have for all large t,

$$Y'(t) \le -r_3Y^2(t) + a_{31}M_2^x e^{\tau(-r_2-\alpha_2 L_1^x)}Y(t-\tau),$$

where $M_2^x = \frac{r_1 - a_{13}L_1^Y}{a_{11}} + \varepsilon_2^x$. Comparison implies that there exists sufficiently small ε_2^Y; $\varepsilon_1^Y > \varepsilon_2^Y > 0$ such that for all large t,

$$Y(t) \le \frac{a_{31}M_2^x e^{\tau(-r_2-\alpha_2 L_1^x)}}{r_3} + \varepsilon_2^Y.$$

Let $M_2^Y = \frac{a_{31}M_2^x e^{\tau(-r_2-\alpha_2 L_1^x)}}{r_3} + \varepsilon_2^Y$. Repeating the above procedure gives the four sequences $\{M_n^x\}$, $\{M_n^Y\}$, $\{L_n^x\}$, and $\{L_n^Y\}$ satisfying

$$\begin{aligned}
M_n^x &= \frac{r_1 - a_{13}L_{n-1}^Y}{a_{11}} + \varepsilon_n^x, &\quad& \varepsilon_1^x > \cdots > \varepsilon_{n-1}^x > \varepsilon_n^x > \cdots > 0,\\
M_n^Y &= \frac{a_{31}M_n^x e^{\tau(-r_2-\alpha_2 L_{n-1}^x)}}{r_3} + \varepsilon_n^Y, && \varepsilon_1^Y > \cdots > \varepsilon_{n-1}^Y > \varepsilon_n^Y > \cdots > 0,\\
L_n^x &= \frac{r_1 - a_{13}M_n^Y}{a_{11}} - \delta_n^x, && \delta_1^x > \cdots > \delta_{n-1}^x > \delta_n^x > \cdots > 0,\\
L_n^Y &= \frac{a_{31}L_n^x e^{\tau(-r_2-\alpha_2 M_n^x)}}{r_3} - \delta_n^Y, && \delta_1^Y > \cdots > \delta_{n-1}^Y > \delta_n^Y > \cdots > 0,
\end{aligned} \tag{6}$$

where the case $n = 1$ for M_n^x and M_n^Y corresponds to $M_1^x = \frac{r_1}{a_{11}} + \varepsilon_1^x$ and $M_1^Y = \frac{a_{31}M_1^x e^{-r_2\tau}}{r_3} + \varepsilon_1^Y$. Furthermore, all solutions $(x(t), Y(t))$ of (4) satisfy

$$L_n^x \le x(t) \le M_n^x, \qquad L_n^Y \le Y(t) \le M_n^Y \tag{7}$$

for all large t. We may assume that all of sequences $\{\varepsilon_n^x\}$, $\{\varepsilon_n^Y\}$, $\{\delta_n^x\}$, and $\{\delta_n^Y\}$ tend to 0 as $n \to \infty$. Since $L_1^x > 0$, we can show that $\{M_n^x\}$, $\{M_n^Y\}$ are bounded decreasing sequences and $\{L_n^x\}$, $\{L_n^Y\}$ are bounded increasing sequences. Thus, there exist M_*^x, M_*^Y, L_*^x, and L_*^Y such that $\lim_{n\to\infty} M_n^x = M_*^x$, $\lim_{n\to\infty} M_n^Y = M_*^Y$, $\lim_{n\to\infty} L_n^x = L_*^x$, and $\lim_{n\to\infty} L_n^Y = L_*^Y$. Letting $n \to \infty$ for (6), we have

$$\begin{aligned}
M_*^x &= \frac{r_1 - a_{13}L_*^Y}{a_{11}}, &\qquad M_*^Y &= \frac{a_{31}M_*^x e^{\tau(-r_2-\alpha_2 L_*^x)}}{r_3},\\
L_*^x &= \frac{r_1 - a_{13}M_*^Y}{a_{11}}, & L_*^Y &= \frac{a_{31}L_*^x e^{\tau(-r_2-\alpha_2 M_*^x)}}{r_3}.
\end{aligned}$$

We can show that

$$M_*^x = L_*^x, \qquad M_*^Y = L_*^Y. \tag{8}$$

Let $x^* = M_*^x = L_*^x$ and $Y^* = M_*^Y = L_*^Y$. Then, we can easily check that these satisfy

$$\begin{aligned}
r_1 - a_{11}x^* - a_{13}Y^* &= 0,\\
-r_3Y^* + a_{31}x^* e^{\tau(-r_2-\alpha_2 x^*)} &= 0.
\end{aligned}$$

This, together with (7) and (8), implies that (x^*, Y^*) is a unique interior equilibrium point which attracts all solutions $(x(t), Y(t))$ of (4) as $t \to +\infty$.

Since (4) has a unique interior equilibrium (x^*, Y^*), (3) has a unique interior equilibrium that corresponds to (x^*, Y^*). Define (x^*, y^*, Y^*) as such an interior equilibrium point of (3). It is easy to prove that the interior equilibrium (x^*, y^*, Y^*) attracts all solutions of (3) if (x^*, Y^*) attracts all solutions of (4). In fact, for any $\varepsilon > 0$,

$$|x(t) - x^*| < \varepsilon, \qquad |x(t)Y(t) - x^*Y^*| < \varepsilon$$

hold for all sufficiently large $t > 0$. From the second expression of (3) we have for all sufficiently large t,

$$y'(t) \le [-r_2 - \alpha_2(x^* - \varepsilon)]y(t) + a_{31}(x^*Y^* + \varepsilon) - a_{31}(x^*Y^* - \varepsilon)e^{[-r_2-\alpha_2(x^*-\varepsilon)]\tau}$$

and

$$y'(t) \ge [-r_2 - \alpha_2(x^* + \varepsilon)]y(t) + a_{31}(x^*Y^* - \varepsilon) - a_{31}(x^*Y^* + \varepsilon)e^{[-r_2-\alpha_2(x^*+\varepsilon)]\tau}.$$

Hence, it follows from comparison and the arbitrariness of ε that

$$\limsup_{t\to+\infty} y(t) \le \frac{a_{31}x^*Y^*\left[1 - e^{(-r_2-\alpha_2 x^*)\tau}\right]}{r_2 + \alpha_2 x^*} = y^*.$$

Similarly, we have $\liminf_{t\to+\infty} y(t) \ge y^*$. Therefore,

$$y^* \le \liminf_{t\to+\infty} y(t) \le \limsup_{t\to+\infty} y(t) \le y^*,$$

which implies $\lim_{t\to+\infty} y(t) = y^*$. The proof is thus completed.

Remark 1. Although one cannot solve interior equilibria of (3) in any explicit forms of parameters when $\alpha_1 = 0$ and $\alpha_2 > 0$, the method used in the proof above makes it possible to show that (3) has a unique global attractive interior equilibrium.

3. Local Stability of an Interior Equilibrium

In this section, we will prove Theorem 2.

Proof. By Theorem 1, (3) has a unique interior equilibrium that attracts all the solutions for all $\tau > \tau_0$. Let (x^*, y^*, Y^*) be such a unique interior equilibrium of (3). Then, obviously, (x^*, Y^*) is a unique interior equilibrium of (4). To prove that (x^*, y^*, Y^*) is locally stable for (3), we have to be concerned with the local stability of (x^*, Y^*) for (4).

Linearizing (4) around (x^*, Y^*), we have

$$\begin{aligned} x'(t) &= x^*[-a_{11}x(t) - a_{13}Y(t)], \\ Y'(t) &= -2r_3Y^*Y(t) \\ &\quad + a_{31}e^{(-r_2-\alpha_2 x^*)\tau}\left[Y^*x(t-\tau) + x^*Y(t-\tau) - \alpha_2 x^*Y^*\int_{t-\tau}^{t} x(s)ds\right], \end{aligned}$$

and we get the characteristic equation of the form

$$\begin{aligned} &\lambda^2 + (a_{11}x^* + 2r_3Y^*)\lambda + 2a_{11}r_3x^*Y^* + [r_3Y^*(a_{13}Y^* - a_{11}x^*) - r_3Y^*\lambda]\,e^{-\lambda\tau} \\ &\qquad - a_{13}\alpha_2 r_3 x^*(Y^*)^2 e^{-\lambda t}\int_{t-\tau}^{t} e^{\lambda s}ds = 0. \end{aligned} \tag{9}$$

One can see that 0 is not a root of the characteristic equation. In fact, otherwise, we obtain

$$\frac{a_{11}r_3}{a_{13}a_{31}e^{-r_2\tau}} = (\alpha_2 x^*\tau - 1)e^{-\alpha_2 x^*\tau}.$$

The right-hand side is less than 1, but the left-hand side is greater than 1 for all $\tau > \tau_0$ because of our assumption. This is a contradiction. Hence, the characteristic equation (9) is reduced to

$$\lambda^2 + p\lambda + q + \frac{r}{\lambda} + \left[s\lambda + u + \frac{v}{\lambda}\right]e^{-\lambda\tau} = 0, \tag{10}$$

where $p = a_{11}x^* + 2r_3Y^*$, $q = 2a_{11}r_3x^*Y^*$, $r = -a_{13}\alpha_2 r_3 x^*(Y^*)^2$, $s = -r_3Y^*$, $u = r_3Y^*(a_{13}Y^* - a_{11}x^*)$, and $v = a_{13}\alpha_2 r_3 x^*(Y^*)^2$ since

$$e^{-\lambda t}\int_{t-\tau}^{t} e^{\lambda s}ds = \frac{1}{\lambda}(1 - e^{-\lambda\tau}).$$

When $\alpha_2 = 0$, one can show that all characteristic roots of (10) have negative real parts for all $\tau > 0$ since $3a_{11}r_3 \geq a_{13}a_{31}$ (see [9]). We will prove that all the characteristic roots have negative real parts for $\alpha_2 > 0$ and all $\tau > \tau_0$, which implies that (x^*, Y^*) is locally asymptotically stable for (4). Assuming the contrary, there exists a characteristic root of (10) on the imaginary axis of the complex plane for some $\alpha_2 = \alpha > 0$ (see [5]). Let $\lambda = i\omega$ ($\omega \neq 0$) be such a characteristic root. Substituting $(\lambda, \alpha_2) = (i\omega, \alpha)$ into (10) and separating the real and imaginary parts, we obtain

$$\begin{aligned}
\left[(-s\omega^2 + v)^2 + (u\omega)^2\right]\cos(\omega\tau) &= (p\omega^2 - r)(-s\omega^2 + v) + u\omega^2(\omega^2 - q)\\
\left[(-s\omega^2 + v)^2 + (u\omega)^2\right]\sin(\omega\tau) &= \omega(s\omega^2 - v)(\omega^2 - q) + u\omega(p\omega^2 - r).
\end{aligned}$$

Squaring and adding the two equations yields

$$\begin{aligned}
\left[(-s\omega^2 + v)^2 + (u\omega)^2\right]^2 = &\left[(p\omega^2 - r)(-s\omega^2 + v) + u\omega^2(\omega^2 - q)\right]^2\\
&+ \left[\omega(s\omega^2 - v)(\omega^2 - q) + u\omega(p\omega^2 - r)\right]^2.
\end{aligned} \tag{11}$$

Define the function

$$\begin{aligned}
f(\Omega) = &\left[(-s\Omega + v)^2 + u^2\Omega\right]^2 - \left[(p\Omega - r)(-s\Omega + v) + u\Omega(\Omega - q)\right]^2\\
&- \Omega\left[(s\Omega - v)(\Omega - q) + u(p\Omega - r)\right]^2.
\end{aligned} \tag{12}$$

Then f is a quintic function such that $f \to -\infty$ as $|\Omega| \to +\infty$ and must have a positive zero $\Omega = \omega^2$ because of (11) and $\omega \neq 0$. Note that $r = -v$. Computing f, we have

$$f(\Omega) = \Omega\left[F(\Omega)G(\Omega) + H(\Omega)\right],$$

where

$$\begin{aligned}
F(\Omega) &= (s^2 + u - ps)\Omega^2 + (u^2 - 2sv + pv + rs - uq)\Omega + v(v - r),\\
G(\Omega) &= (s^2 - u + ps)\Omega + u^2 - 2sv - pv - rs + uq,\\
H(\Omega) &= -\left[s\Omega^2 + (up - sq - v)\Omega + vq - ur\right]^2.
\end{aligned}$$

Clearly, $H(\Omega) \le 0$. It is shown that $F(\Omega) > 0$ for $\Omega > 0$ because

$$\begin{aligned} F(\Omega) &= r_3(Y^*)^2(a_{13} + 3r_3)\Omega^2 \\ &\quad + r_3(Y^*)^2[r_3(a_{13}Y^* - a_{11}x^*)(a_{13}Y^* - 3a_{11}x^*) + a_{13}\alpha_2 x^*(a_{11}x^* + 5r_3Y^*)]\Omega \\ &\quad + 2\left[a_{13}\alpha_2 r_3 x^*(Y^*)^2\right]^2, \end{aligned}$$

and

$$a_{13}Y^* - 3a_{11}x^* < a_{13}Y^* - a_{11}x^* \le \frac{x^*}{r_3}\left(a_{13}a_{31}e^{-r_2\tau} - r_3 a_{11}\right) < 0. \tag{13}$$

It is also shown that $G(\Omega) < 0$ for $\Omega > 0$ because

$$\begin{aligned} G(\Omega) &= -r_3(Y^*)^2(a_{13} + r_3)\Omega \\ &\quad + r_3(Y^*)^2\left[r_3\left\{(a_{13}Y^*)^2 - (a_{11}x^*)^2\right\} - a_{13}\alpha_2 x^*(a_{11}x^* + r_3Y^*)\right], \end{aligned}$$

and $(a_{13}Y^*)^2 - (a_{11}x^*)^2 < 0$ by (13). Hence, $f(\Omega) < 0$ for $\Omega > 0$. This implies that there are no positive roots of $f(\Omega) = 0$, which is a contradiction. Therefore, (x^*, Y^*) is locally asymptotically stable for (4).

We can easily prove that the interior equilibrium (x^*, y^*, Y^*) of (3) is locally stable if (x^*, Y^*) is locally stable for (4). In fact, for any $\varepsilon > 0$, suppose that $y(0)$ satisfies

$$|y(0) - y*| < \frac{\varepsilon}{3}.$$

Then, there exists a sufficiently small $\varepsilon > \varepsilon_1 > 0$ such that

$$|y(0) - y^*_{\varepsilon_1+}| < \frac{\varepsilon}{2}, \qquad |y(0) - y^*_{\varepsilon_1-}| < \frac{\varepsilon}{2}, \tag{14}$$

and also such that

$$|y^*_{\varepsilon_1+} - y^*| < \frac{\varepsilon}{2}, \qquad |y^*_{\varepsilon_1-} - y^*| < \frac{\varepsilon}{2}, \tag{15}$$

where

$$\begin{aligned} y^*_{\varepsilon_1+} &= \frac{a_{31}(x^*Y^* + \varepsilon_1) - a_{31}(x^*Y^* - \varepsilon_1)e^{[-r_2-\alpha_2(x^*+\varepsilon_1)]}}{r_2 + \alpha_2(x^* - \varepsilon_1)}, \\ y^*_{\varepsilon_1-} &= \frac{a_{31}(x^*Y^* - \varepsilon_1) - a_{31}(x^*Y^* + \varepsilon_1)e^{[-r_2-\alpha_2(x^*-\varepsilon_1)]}}{r_2 + \alpha_2(x^* + \varepsilon_1)}. \end{aligned}$$

Since $x(t)$ and $Y(t)$ are locally asymptotically stable to x^* and Y^* respectively, we can choose $\delta_1 > 0$ and $\delta_2 > 0$ such that for $t \ge 0$,

$$|x(t) - x^*| < \varepsilon_1, \quad |Y(t) - Y^*| < \varepsilon_1, \quad |x(t)Y(t) - x^*Y^*| < \varepsilon_1$$

hold if $|x(0) - x^*| < \delta_1$ and $|Y(0) - Y^*| < \delta_2$. Thus, from the second expression of (3) we have for any $t \ge 0$,

$$\begin{aligned} y'(t) &\le [-r_2 - \alpha_2(x^* - \varepsilon_1)]y(t) + a_{31}(x^*Y^* + \varepsilon_1) - a_{31}(x^*Y^* - \varepsilon_1)e^{[-r_2-\alpha_2(x^*+\varepsilon_1)]\tau} \\ y'(t) &\ge [-r_2 - \alpha_2(x^* + \varepsilon_1)]y(t) + a_{31}(x^*Y^* - \varepsilon_1) - a_{31}(x^*Y^* + \varepsilon_1)e^{[-r_2-\alpha_2(x^*-\varepsilon_1)]\tau} \end{aligned}$$

if $|x(0)-x^*|<\delta_1$ and $|Y(0)-Y^*|<\delta_2$ hold. Hence, it follows from comparison that for $t\geq 0$,

$$|y(t)-y^*|\leq \max_{t\geq 0}\{B_{\varepsilon_1+}(t), B_{\varepsilon_1-}(t)\}$$

where

$$B_{\varepsilon_1+}(t)=|y(0)-y^*_{\varepsilon_1+}|e^{[-r_2-\alpha_2(x^*-\varepsilon_1)]t}+|y^*_{\varepsilon_1+}-y^*|,$$
$$B_{\varepsilon_1-}(t)=|y(0)-y^*_{\varepsilon_1-}|e^{[-r_2-\alpha_2(x^*+\varepsilon_1)]t}+|y^*_{\varepsilon_1-}-y^*|.$$

From (14) and (15), we obtain for $t\geq 0$,

$$|y(t)-y^*|<\frac{\varepsilon}{2}\max_{t\geq 0}\{e^{[-r_2-\alpha_2(x^*-\varepsilon_1)]t}, e^{[-r_2-\alpha_2(x^*+\varepsilon_1)]t}\}+\frac{\varepsilon}{2}<\varepsilon.$$

This completes the proof.

5. Discussion

We considered a time-delay model for inverse trophic relationship based on the model proposed in [1, 9]. Global attractivity and local stability were discussed for an interior equilibrium of the system with $\alpha_1=0$ and $\alpha_2>0$. To prove Theorem 1, we used two kinds of comparison and constructed four sequences corresponding to eventual upper and lower bounds of solutions. The positiveness of L_x^1 is essencial to global attractivity for the interior equilibrium. We also obtained a condition under which the interior equilibrium is globally asymptotically stable. Theorems 1 and 2 show that α_2 is not *destabilizer* for global properties of the interior equilibrium under the conditions that ensure global attractivity or global asymptotic stability in the case $\alpha_1=\alpha_2=0$. This may suggest that α_2 maintains global properties and does not cause global bifurcation of solutions for (3).

Taking $\alpha_1>0$ into consideration, we actually conjecture that a new interior equilibrium will appear to become stable and the originary interior equilibrium will be destabilized. A more sophisticated mathematical approach and more tedious calculation are required to solve the conjecture, which is left for future work.

Acknowledgments

The authors would like to thank Professor T. Namba of Osaka Women's University for his useful comments on references for inverse trophic relationship.

References

[1] W.G. Aiello, H.I. Freedman, A time-delay model of single-species growth with stage structure, *Math. Biosci.*, **101** (1990) 139-153.

[2] W.G. Aiello, H.I. Freedman, J. Wu, Analysis of a model representing stage-structured population growth with state-dependent time delay, *SIAM J. Appl. Math.*, **52** (1992) 855-869.

[3] R. P. Garcia and R.V. Alejandre, Predation upon Larvae of the Pacific sardine *Sardinops Sagax* by Cyclopoid Copepods, *J. Crustacean Biology*, **15**, (1995) 196-201.

[4] H. J. Jeong, Predation by the heterotrophic dinoflagellate *Protoperidinium Cf. divergens* on copepod eggs and early naupliar stages, *Mar. Ecol. Prog. Ser.*, **114**, (1994) 203-208.

[5] Y. Kuang, "Delay Differential Equations with Applications in Population Dynamics," Academic Press, New York, 1993.

[6] M. V. Lebour, The food of plankton organisms II, *J. Mar. Biol. Assoc.*, U. K., (1923) 70-92.

[7] K. Lillenlund and R. Lasker, Laboratory studies of predation by marine copepods on fish larvae, *Fishery Bulletin*, **69**, (1971) 655-667.

[8] S. Liu, L. Chen, G. Luo, Y. Jiang, Asymptotic behaviors of competitive Lotka-Volterra system with stage structure, *J. Math. Anal. Appl.*, **271**, (2002) 124-138.

[9] Y. Saito and Y. Takeuchi, A time-delay model for prey-predator growth with stage structure, to appear.

[10] X. Song, L. Chen, Optimal harvesting and stability for a two species competitive system with stage structure, *Math. Biosci.*, **170** (2001) 173-186.

[11] W. Wang, L. Chen, A predator-prey system with stage-structure for predator, *Comput. Math. Appl.*, **33** (1997) 83-91.