



A model for the growth of a population exhibiting stage structure: cannibalism and cooperation [☆]

H.I. Freedman ^{a,*}, Joseph W.-H. So ^a, Jianhong Wu ^b

^a *Applied Mathematics Institute, Department of Mathematics, University of Alberta, Edmonton, Alta., Canada T6G 2G1*

^b *Department of Mathematics and Statistics, York University, North York, Ont., Canada M3J 1P3*

Received 8 March 1992

Abstract

A model of a stage-structured population with fixed maturity time for the immature stage and interaction terms that may be interpreted as cooperation or cannibalism is proposed. The existence and stability of the equilibrium set are discussed. In the case of cannibalism, it is shown by a numerical example how a Hopf bifurcation could result in a stable periodic solution.

Keywords: Cannibalism; Cooperation; Equilibrium; Hopf bifurcation; Periodic solution; Single species; Stability; Stage structure; Time delay

1. Introduction and model equations

We propose a model of a single-species population with stage structure consisting of immature and mature stages as the following system of retarded functional differential equations:

$$\begin{cases} \dot{x}(t) = -\gamma x(t) - \alpha y(t - \tau)e^{-\gamma\tau} + \alpha y(t) + cx(t)y(t), & (1.1a) \\ \dot{y}(t) = \alpha y(t - \tau)e^{-\gamma\tau} - \beta y^2(t) + dx(t)y(t), & (1.1b) \end{cases}$$

where x and y denote the concentration of immature and mature populations, respectively. The model is derived under the following assumptions.

(H1) The birth rate into the immature population is proportional to the existing mature population with a proportionality constant $\alpha > 0$ (cf. the term $\alpha y(t)$ in (1.1a)).

[☆] Research partially supported by grants from the Natural Sciences and Engineering Research Council of Canada.

* Corresponding author.

(H2) The death rate of the immature population is proportional to the existing immature population with a proportionality constant $\gamma > 0$ (cf. the term $-\gamma x(t)$ in (1.1a)).

(H3) The death rate of the mature population is of a logistic nature, i.e., it is proportional to the square of the population with a proportionality constant $\beta > 0$ (cf. the term $-\beta y^2(t)$ in (1.1b)).

(H4) The length of time from birth to maturity is a constant $\tau > 0$. Those immature individuals born at time $t - \tau$ and surviving to time t , namely $\alpha y(t - \tau)e^{-\gamma\tau}$, exit from the immature population and enter into the mature population.

(H5) The immature and the mature populations interact with each other in a bilinear fashion (cf. the term $cx(t)y(t)$ in (1.1a) and the term $dx(t)y(t)$ in (1.1b)).

The case when c and d are both zero was studied in [1]. In that case, (1.1b) contains no x terms and is a scalar retarded functional differential equation with a positive feedback delay term. Hence it defines an eventually strongly monotone semiflow (cf. [15]). When $c = d = 0$, there are two equilibria: $y = 0$ and $y = y^* = \alpha e^{-\gamma\tau}/\beta$ for (1.1b), and, using the characteristic equation, it is easily seen that $y = 0$ is unstable and $y = y^*$ is asymptotically stable. Therefore, by applying [11, Theorem 10.3], we conclude that $y(t) \rightarrow y^*$ as $t \rightarrow \infty$, provided $y(t) \geq 0$ is not identically zero on $[-\tau, 0]$. Moreover, on solving (1.1a), one obtains

$$x(t) = e^{-\gamma t} \left[x(0) - \alpha \int_{-\tau}^0 y(\theta) e^{\gamma\theta} d\theta \right] + \alpha e^{-\gamma t} \int_{t-\tau}^t y(\theta) e^{\gamma\theta} d\theta,$$

from which it follows that $x(t) \rightarrow \alpha(1 - e^{-\gamma\tau})y^*/\gamma$ as $t \rightarrow \infty$. Hence, solutions $(x(t), y(t))$ of (1.1) converge to the (unique) positive equilibrium $E^* = (x^*, y^*) = (\alpha(1 - e^{-\gamma\tau})y^*/\gamma, y^*)$.

In the cases where $c \neq 0$ and $d \neq 0$, the net effects of the two stages on each other are given by the signs of c and d . In the case $c > 0$, $d > 0$, there is a net effect of cooperation between immatures and adults in the population. Intrinsically, this is what one would expect in many cases in nature, although this seems not be treated in the modelling literature.

The case where $c < 0$, $d > 0$ may be thought of as a first approximation to modelling cannibalism. Models of cannibalism (mostly egg cannibalism) have been considered in the literature (see [4,6,9,10,14]). However, the above-mentioned papers mostly contain models more simplistic than the one considered here.

The main purpose of this paper is to discuss the structure of the equilibrium point set, the local stability of each equilibrium and the existence of Hopf bifurcation for system (1.1). In Section 2, we consider the cannibalism case, i.e., $c < 0$, $d > 0$. It will be shown that infinitely many nonconstant periodic solutions bifurcate from the unique positive equilibrium point when α , β , c , γ and τ are kept fixed and d increases unboundedly, through a sequence of Hopf bifurcations. Also a numerical example is presented which shows that the first Hopf bifurcation is supercritical and a stable periodic solution is bifurcated from the positive equilibrium as the latter loses its stability. The case of cooperation, i.e., $c, d > 0$, is considered in Section 3. We will demonstrate how the number of positive equilibria undergoes a series of changes from 0 to 2 when three parameters (determined explicitly by the coefficients of (1.1)) vary. Stability analysis in some typical cases are also carried out and it shows that a Hopf bifurcation is unlikely. Proofs of the main results in Sections 2 and 3 are postponed to Appendices A and B, respectively. Finally, a discussion of our results is given in Section 4.

We emphasize that the models considered here are only first approximations to modelling cooperation and cannibalism in populations with stage structure, i.e., time delays in the cooperation or cannibalistic effects are ignored and the effects of cooperation and cannibalism on survivability to maturity are not taken into account.

2. The case of cannibalism

In this section, we consider the case when $c < 0$ and $d > 0$ in (1.1). For convenience of notation, we will rewrite (1.1) as

$$\begin{cases} \dot{x}(t) = -\gamma x(t) - \alpha y(t - \tau)e^{-\gamma\tau} + \alpha y(t) - cx(t)y(t), \\ \dot{y}(t) = \alpha y(t - \tau)e^{-\gamma\tau} - \beta y^2(t) + dx(t)y(t), \end{cases} \tag{2.1}$$

and keep $c > 0$.

Let $\bar{E} = (\bar{x}, \bar{y})$ denote a nonnegative equilibrium point of (2.1), i.e., $\bar{x}, \bar{y} \geq 0$. Then (\bar{x}, \bar{y}) must satisfy the algebraic equations

$$-\gamma x - \alpha ye^{-\gamma\tau} + \alpha y - cxy = 0, \quad \alpha ye^{-\gamma\tau} - \beta y^2 + dx = 0. \tag{2.2}$$

Clearly, $E_0 = (0, 0)$ is an equilibrium and there are no other equilibria lying on the x - nor on the y -axis.

To find the other positive equilibria, i.e., $\bar{x}, \bar{y} > 0$, we factor out y from the second equation of (2.2) and rewrite the equations in (2.2) as

$$y = \frac{d}{\beta}x + \frac{\alpha}{\beta}e^{-\gamma\tau}, \quad y = \frac{\gamma x}{\alpha(1 - e^{-\gamma\tau}) - cx}. \tag{2.3}$$

Denote the graphs of these two functions by Γ_1 and Γ_2 , respectively.

For $0 < x < \alpha(1 - e^{-\gamma\tau})/c$, we have

$$\begin{aligned} \frac{\gamma x}{\alpha(1 - e^{-\gamma\tau}) - cx} &> 0, \\ \frac{d}{dx} \left[\frac{\gamma x}{\alpha(1 - e^{-\gamma\tau}) - cx} \right] &= \frac{\alpha\gamma(1 - e^{-\gamma\tau})}{(\alpha(1 - e^{-\gamma\tau}) - cx)^2} > 0 \end{aligned}$$

and

$$\frac{d^2}{dx^2} \left[\frac{\gamma x}{\alpha(1 - e^{-\gamma\tau}) - cx} \right] = \frac{2\alpha\gamma c(1 - e^{-\gamma\tau})}{(\alpha(1 - e^{-\gamma\tau}) - cx)^3} > 0.$$

Thus, Γ_2 is a continuous, concave (upwards) curve and increases monotonically from 0 to $+\infty$ as x increases from 0 to $\alpha(1 - e^{-\gamma\tau})/c$. On the other hand, Γ_1 is a horizontal (respectively decreasing, respectively increasing) line, depending on whether d is zero (respectively negative, respectively positive) (see Fig. 1). Hence, Γ_1 and Γ_2 have one and only one intersection in the positive quadrant of the x - y -plane. Consequently, (2.1) has a unique positive equilibrium $E^* = (x^*, y^*)$.

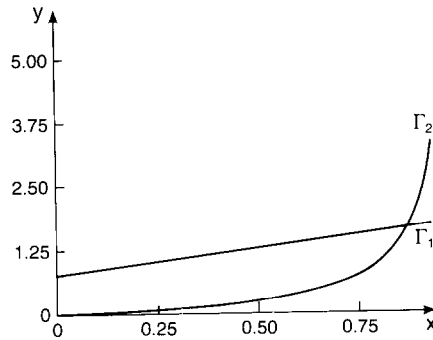


Fig. 1. $\alpha = 1, \beta = 1, c = 1, d = 1, \gamma = \frac{1}{4}$ and $\tau = 1$.

In fact, from the second equation of (2.3), we have

$$x^* = \frac{\alpha(1 - e^{-\gamma\tau})y^*}{\gamma + cy^*}.$$

Substituting this into the first equation of (2.3), one obtains

$$\beta cy^{*2} = \gamma\alpha e^{-\gamma\tau} + [c\alpha e^{-\gamma\tau} - \beta\gamma + d\alpha(1 - e^{-\gamma\tau})]y^*.$$

By solving this quadratic equation in y^* , it follows that the positive equilibrium E^* can be expressed explicitly in terms of the coefficients of (2.1) as follows:

$$y^* = \frac{1}{2} \left(\theta + \sqrt{\theta^2 + \frac{4\alpha\gamma}{\beta c} e^{-\gamma\tau}} \right), \quad x^* = \frac{\alpha(1 - e^{-\gamma\tau})}{\gamma + cy^*} y^*, \tag{2.4}$$

where

$$\theta = \frac{1}{\beta c} [c\alpha e^{-\gamma\tau} - \beta\gamma + d\alpha(1 - e^{-\gamma\tau})]. \tag{2.5}$$

For later purposes (see Lemma A.1), we also observe that $\theta = \alpha(1 - e^{-\gamma\tau})d/(\beta c) + o(d)$, $y^* = \alpha(1 - e^{-\gamma\tau})d/(\beta c) + o(d)$ and $x^* = \alpha(1 - e^{-\gamma\tau})/c + o(1)$, as d tends to $+\infty$.

To determine the local stability of the equilibria E_0 and E^* , we linearized (2.1) about $\tilde{E} = (\tilde{x}, \tilde{y})$ (\tilde{E} may be E_0 or E^*):

$$\begin{cases} \dot{X}(t) = -(\gamma + c\tilde{y})X(t) - \alpha Y(t - \tau)e^{-\gamma\tau} + \alpha Y(t) - c\tilde{x}Y(t), \\ \dot{Y}(t) = d\tilde{y}X(t) + \alpha Y(t - \tau)e^{-\gamma\tau} - 2\beta\tilde{y}Y(t) + d\tilde{x}Y(t). \end{cases}$$

The corresponding characteristic equation (in the unknown λ) is

$$\det \begin{pmatrix} \lambda + \gamma + c\tilde{y} & -\alpha + \alpha e^{-(\lambda + \gamma)\tau} + c\tilde{x} \\ -d\tilde{y} & \lambda + 2\beta\tilde{y} - \alpha e^{-(\lambda + \gamma)\tau} - d\tilde{x} \end{pmatrix} = 0,$$

that is,

$$\lambda^2 + A\lambda + B = De^{-\lambda\tau}(\lambda + F), \tag{2.6}$$

where

$$\begin{aligned} A &= \gamma + c\bar{y} + 2\beta\bar{y} - d\bar{x}, & B &= (\gamma + c\bar{y})(2\beta\bar{y} - d\bar{x}) + d\bar{y}(c\bar{x} - \alpha), \\ D &= \alpha e^{-\gamma\tau}, & F &= \gamma + c\bar{y} - d\bar{y}. \end{aligned} \quad (2.7)$$

For $(\bar{x}, \bar{y}) = E_0$, we have the following theorem.

Theorem 2.1. *The equilibrium point $E_0 = (0, 0)$ is unstable.*

This result can be easily verified. In fact, for $\bar{E} = E_0$, (2.6) reduces to

$$\lambda^2 + \gamma\lambda = \alpha e^{-(\lambda+\gamma)\tau}(\lambda + \gamma) \quad \text{or} \quad (\lambda + \gamma)(\lambda - \alpha e^{-(\lambda+\gamma)\tau}) = 0.$$

Obviously, $\lambda = -\gamma$ is a negative solution of (A.1). It is also easily seen that there exists a positive real number λ_0 such that $\lambda = \lambda_0$ satisfies $\lambda = \alpha e^{-(\lambda+\gamma)\tau}$. Therefore E_0 is unstable.

To determine the local stability of the positive equilibrium E^* , we let $\lambda = u + iv$, $u, v \in \mathbb{R}$, and rewrite (2.6) (with (x^*, y^*) replacing (\bar{x}, \bar{y})) in terms of its real and imaginary parts as

$$\begin{cases} u^2 - v^2 + Au + B = De^{-u\tau}[(u + F)\cos(v\tau) + v \sin(v\tau)], \\ 2uv + Av = De^{-u\tau}[v \cos(v\tau) - (u + F)\sin(v\tau)]. \end{cases} \quad (2.8)$$

When $u = 0$, (2.8) reduces to

$$\begin{cases} -v^2 + B = D[F \cos(v\tau) + v \sin(v\tau)], \\ Av = D[v \cos(v\tau) - F \sin(v\tau)]. \end{cases} \quad (2.9)$$

It follows by taking the sum of squares that

$$(B - v^2)^2 + A^2v^2 = D^2[F^2 + v^2]$$

or

$$v^4 + (A^2 - 2B - D^2)v^2 + B^2 - D^2F^2 = 0. \quad (2.10)$$

Therefore, $\lambda = iv$ is a pure imaginary root of (2.6) if and only if v solves the system of equations

$$v^4 + (A^2 - 2B - D^2)v^2 + B^2 - D^2F^2 = 0, \quad Av = D[v \cos(v\tau) - F \sin(v\tau)]. \quad (2.11)$$

For the remainder of this section, it is useful to consider the parameters α , β , c , γ and τ as fixed and use d as a bifurcation parameter. It will be shown in Appendix A that when $d = 0$, all the roots λ of the characteristic equation (2.6) have negative real parts; and that for d sufficiently small, (2.10) has no real root v . Therefore, for sufficiently small d , (2.6) has no solution with nonnegative real part. This implies the following.

Theorem 2.2. *There exists a constant $d_0 = d_0(\alpha, \beta, \gamma, c, \tau) > 0$ such that for $0 \leq d < d_0$, the corresponding positive equilibrium E^* is (locally) asymptotically stable.*

We will also show in Appendix A that, provided τ is small enough, for certain large (positive) values of d , the characteristic equation (2.6) has a pair of purely imaginary roots. This then

leads to a Hopf bifurcation of nonconstant positive periodic solutions of (2.1) bifurcating from the positive equilibrium E^* . The precise statement can be formulated as follows.

Theorem 2.3. *Assume that $0 \leq \tau < \ln(2)/\gamma$. Then there exists an unbounded sequence of positive numbers $d_1 < d_2 < \dots < d_j < \dots$ such that the characteristic equation (2.6) at $d = d_j$, $j = 1, 2, \dots$, has a pair of purely imaginary roots $\pm i\nu(d_j)$ such that $(\nu(d_j) - \delta d_j)/d_j \rightarrow 0$ as $j \rightarrow \infty$. Here δ is a positive constant defined by*

$$\delta^2 = \frac{1}{2} \left(\frac{\alpha}{\beta c} \right)^2 (1 - e^{-\gamma\tau}) \times \left\{ \left([(\beta + c)^2(1 - e^{-\gamma\tau}) + 2\beta c(2e^{-\gamma\tau} - 1)]^2 + 4(\beta c)^2(1 - e^{-\gamma\tau})(3e^{-\gamma\tau} - 1) \right)^{1/2} - [(\beta + c)^2(1 - e^{-\gamma\tau}) + 2\beta c(2e^{-\gamma\tau} - 1)] \right\}. \tag{2.12}$$

In addition, for each j , there exist two sequences of positive numbers $\{d_j^n\}_{n=1}^\infty$ and $\{v_j^n\}_{n=1}^\infty$ and a sequence of positive $(2\pi/v_j^n)$ -periodic solutions $\{(x_j^n(t), y_j^n(t))\}_{n=1}^\infty$ of (2.1) with $d = d_j^n$ such that $d_j^n \rightarrow d_j$ and $v_j^n \rightarrow \nu(d_j)$ as $n \rightarrow \infty$.

As a numerical example, we fix $\alpha = \beta = c = \tau = 1$, $\gamma = \frac{1}{4}$ and use $d \geq 0$ as a bifurcation parameter. By solving the first equation in (2.11) for ν in terms of d , we get $\nu(d)$. Substituting this $\nu(d)$ into the second equation in (2.11) for ν , we obtain one equation in the unknown d . Using MAPLE (a symbolic/algebraic manipulation language), it is discovered that $d^* = 4.564100754$ is the first positive root of this equation. Hence d^* is the parameter value at which the first Hopf bifurcation from the equilibrium E^* occurs. Moreover, it is also found that $E^* = (0.192184952, 1.655952267)$ at $d = d^*$.

Feeding the above information into Hassard’s BIFDD program for Hopf bifurcation of delay equations, we obtain $\mu_2 = 1.380956858$, $\tau_2 = 5.70141118$, $\beta_2 = -0.4485837677$, $\text{Re}(c_1(0)) = -0.224291838$ and $\text{Im}(c_1(0)) = -5.108486717$. (See [8] for the meaning of these values.) Thus, we have a supercritical Hopf bifurcation at $d = d^*$ and the bifurcated periodic solutions are stable. Also, BIFDD tells us that there are two eigenvalues crossing the imaginary axis and the remaining eigenvalues have negative real parts.

As a further check, we use a delay equation solver supplied by Paul Waltman and solve (2.1) with $d = 4.6$ and the initial conditions $x(0) = 0.2$ and $y(\theta) = 2.0$ for $-1 \leq \theta \leq 0$. The result is given in Fig. 2, which shows that there is a periodic solution.

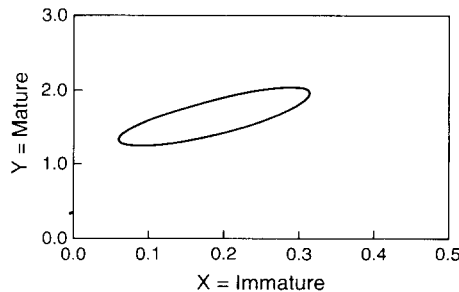


Fig. 2. $\alpha = 1$, $\beta = 1$, $c = 1$, $d = 4.6$, $\gamma = \frac{1}{4}$ and $\tau = 1$.

3. The case of cooperation

In this section, we will consider the case when $c > 0$ in (1.1), i.e.,

$$\begin{cases} \dot{x}(t) = -\gamma x(t) - \alpha y(t - \tau)e^{-\gamma\tau} + \alpha y(t) + cx(t)y(t), \\ \dot{y}(t) = \alpha y(t - \tau)e^{-\gamma\tau} - \beta y^2(t) + dx(t)y(t), \end{cases} \quad (3.1)$$

where $c > 0$ and $d > 0$.

Clearly, $E_0 = (0, 0)$ is an equilibrium of (3.1) and there are no other nonnegative equilibria on the x - nor y -axis other than E_0 . Let $E^* = (x^*, y^*)$ denote a positive equilibrium of (3.1). Then,

$$-\gamma x^* - \alpha y^* e^{-\gamma\tau} + \alpha y^* + cx^* y^* = 0, \quad \alpha e^{-\gamma\tau} - \beta y^* + dx^* = 0. \quad (3.2)$$

First, we state a result on the number of positive equilibrium points of (3.1). Its proof is given in Appendix B.

Theorem 3.1. *Let*

$$p = \frac{\beta\gamma - \alpha d}{\beta c} + \frac{\alpha}{\beta c}(c + d)e^{-\gamma\tau} - 2\sqrt{\frac{\alpha\gamma}{\beta c}e^{-\gamma\tau}},$$

and if $p \geq 0$, define

$$\begin{aligned} q_1 &= p + 2\sqrt{\frac{\alpha\gamma}{\beta c}e^{-\gamma\tau}} - \sqrt{p\left(p + 4\sqrt{\frac{\alpha\gamma}{\beta c}e^{-\gamma\tau}}\right)}, \\ q_2 &= p + 2\sqrt{\frac{\alpha\gamma}{\beta c}e^{-\gamma\tau}} + \sqrt{p\left(p + 4\sqrt{\frac{\alpha\gamma}{\beta c}e^{-\gamma\tau}}\right)}. \end{aligned} \quad (3.3)$$

Then (cf. Figs. 3 and 4),

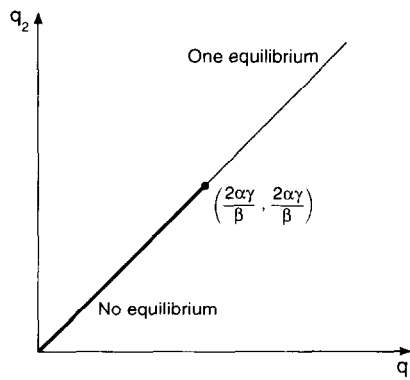


Fig. 3. If $p = 0$, then $q_1 = q_2 = 2\{(\alpha\gamma e^{-\gamma\tau})/(\beta c)\}^{1/2}$.

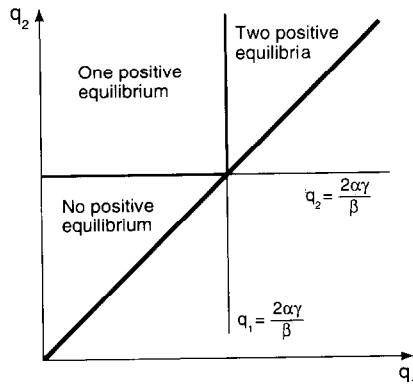


Fig. 4. If $p > 0$, then $q_2 > q_1$.

- (i) if $p < 0$, then (3.1) has no positive equilibrium;
- (ii) if $p = 0$ and $q_1 > 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has one positive equilibrium; if $p = 0$ and $q_1 \leq 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has no positive equilibrium;
- (iii) if $p > 0$ and $q_1 > 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has two positive equilibria; if $p > 0$ and $q_1 \leq 2\alpha e^{-\gamma\tau}/\beta < q_2$, (3.1) has one positive equilibrium; and if $p > 0$ and $q_2 \leq 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has no positive equilibrium.

For τ is sufficiently large, we have the following observation.

Remark 3.2. If $\beta\gamma > \alpha d$, then for sufficiently large τ we have $p > 0$ and, as $\tau \rightarrow \infty$,

$$\begin{aligned} \frac{q_1}{e^{-\gamma\tau}} &= \frac{4\alpha\gamma/(\beta c)}{p + 2\sqrt{\alpha\gamma e^{-\gamma\tau}/(\beta c)} + \sqrt{p(p + 4\sqrt{\alpha\gamma e^{-\gamma\tau}/(\beta c)})}} \\ &\rightarrow \frac{4\alpha\gamma/(\beta c)}{2(\beta\gamma - \alpha d)/(\beta c)} = \frac{2\alpha}{\beta - \alpha d/\gamma} > \frac{2\alpha}{\beta}, \end{aligned}$$

so that $q_1 > 2\alpha e^{-\gamma\tau}/\beta$. Therefore, (3.1) has two positive equilibria.

Similarly, if $\beta\gamma < \alpha d$ and τ is sufficiently large, then $p < 0$ and hence (3.1) has no positive equilibrium.

For $\tau > 0$ sufficiently small, we have the following theorem.

Theorem 3.3. If $\beta\gamma > \alpha c$, then for $\tau > 0$ sufficiently small, (3.1) has two positive equilibria. If $\beta\gamma < \alpha c$ and $\tau > 0$ is sufficiently small, (3.1) has no positive equilibrium.

We now consider the stability of the equilibria. The linearization of (3.1) at an equilibrium point $\bar{E} = (\bar{x}, \bar{y})$ is given by

$$\begin{cases} \dot{X}(t) = [c\bar{y} - \gamma]X(t) + [\alpha + c\bar{x}]Y(t) - \alpha e^{-\gamma\tau}Y(t - \tau), \\ \dot{Y}(t) = d\bar{y}X(t) + [d\bar{x} - 2\beta\bar{y}]Y(t) + \alpha e^{-\gamma\tau}Y(t - \tau). \end{cases} \tag{3.4}$$

The associated characteristic equation is

$$\det \begin{pmatrix} \lambda - (c\bar{y} - \gamma) & -(\alpha + c\bar{x}) + \alpha e^{-\gamma\tau} e^{-\lambda\tau} \\ -d\bar{y} & \lambda - (d\bar{x} - 2\beta\bar{y}) - \alpha e^{-\gamma\tau} e^{-\lambda\tau} \end{pmatrix} = 0,$$

that is,

$$\lambda^2 - [c\bar{y} - 2\beta\bar{y} - \gamma + d\bar{x}]\lambda + [c\bar{y} - \gamma][d\bar{x} - 2\beta\bar{y}] - d\bar{y}[\alpha + c\bar{x}] - \alpha e^{-(\lambda+\gamma)\tau}[\lambda + \gamma - c\bar{y} - d\bar{y}] = 0. \tag{3.5}$$

If $\tilde{E} = E_0$, then (3.5) becomes

$$\lambda^2 + \gamma\lambda - \alpha e^{-(\lambda+\gamma)\tau}[\lambda + \gamma] = 0, \tag{3.6}$$

that is,

$$(\lambda + \gamma)f(\lambda) = 0,$$

where $f(\lambda) = \lambda - \alpha e^{-(\lambda+\gamma)\tau}$. Since $f(0) < 0$ and $f(\infty) = \infty$, there exists $\lambda_0 > 0$ such that $f(\lambda_0) = 0$; so the characteristic equation (3.6) has a positive root. Thus we proved the following theorem.

Theorem 3.4. $(0, 0)$ is unstable.

As we can see from Theorem 3.1, the case when system (3.1) has only one positive equilibrium is not robust, since a small change in the parameters would lead to the case of no positive equilibrium or the case of two equilibria. Therefore, we will only concentrate on the case when system (3.1) has two positive equilibria $E_i^* = (x_i^*, y_i^*)$, $i = 1, 2$, with $y_2^* > y_1^*$. Concerning E_2 , we have the following theorem.

Theorem 3.5. E_2 is unstable.

Some information about the stability of E_1 can be obtained by taking $\tau > 0$ either very large or very small. In the case when τ is large, we have the following theorem.

Theorem 3.6 If $\beta\gamma > \alpha d$ and τ is sufficiently large, then E_1 is asymptotically stable.

In the case when $\tau > 0$ is small, we have the following theorem.

Theorem 3.7 If $\beta\gamma > \alpha(c + \frac{2}{3}d)$ and $\tau > 0$ is sufficiently small, then (3.1) has two positive equilibria: $E_1(x_1^*, y_1^*)$, $E_2(x_2^*, y_2^*)$. E_1 is asymptotically stable and E_2 is unstable.

4. Discussion

In this paper we have considered a model of species growth with stage structure incorporating terms which may be interpreted as net effects one stage upon the other. In particular, we are able to interpret the net effects as cooperation in one case and cannibalism in another. We

were able to carry out a stability analysis of the equilibria and to show by a numerical example that in the case of cannibalism, a Hopf bifurcation could occur.

The models considered here should be viewed as a first attempt to portray net effects of cooperation and cannibalism in continuous population models with stage structure. Clearly more complicated net effect terms are called for in the next models. In particular, one should incorporate the effects of cooperation and cannibalism into the survival of immatures to maturity, and the effect of the time delays on the cooperation and cannibalism. These would certainly lead to more complicated models and will be considered in a future paper.

The case of competitive net effects was not discussed in this paper, since certain complications arise, which suggest that this case should also be discussed in a separate paper.

Appendix A. Proofs of the main results in Section 2

Proof of Theorem 2.2. When $d = 0$, by (2.2), $E^* = (\alpha^2 e^{-\gamma\tau}(1 - e^{-\gamma\tau})/(\gamma\beta + \alpha c e^{-\gamma\tau}), \alpha e^{-\gamma\tau}/\beta)$. Therefore from (2.7) (replacing \tilde{E} by E^*) we have

$$A = \gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} + 2\alpha e^{-\gamma\tau}, \quad B = \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} \right) 2\alpha e^{-\gamma\tau}, \quad D = \alpha e^{-\gamma\tau},$$

$$F = \gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau}.$$

Eq. (2.6) (at $d = 0$ and $\tilde{E} = E^*$) then becomes

$$\lambda^2 + \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} + 2\alpha e^{-\gamma\tau} \right) \lambda + \left(\lambda + c \frac{\alpha}{\beta} e^{-\gamma\tau} \right) (2\alpha e^{-\gamma\tau})$$

$$= \alpha e^{-\gamma\tau} e^{-\lambda\tau} \left(\lambda + \gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} \right),$$

which can be factorized as

$$\left(\lambda + \gamma + \frac{c\alpha}{\beta} e^{-\gamma\tau} \right) (\lambda + 2\alpha e^{-\gamma\tau} - \alpha e^{-\gamma\tau} e^{-\lambda\tau}) = 0.$$

Thus,

$$\lambda + \gamma + \frac{c\alpha}{\beta} e^{-\gamma\tau} = 0 \quad \text{or} \quad \lambda + 2\alpha e^{-\gamma\tau} - \alpha e^{-\gamma\tau} e^{-\lambda\tau} = 0.$$

In either case, we can easily show that $\text{Re}(\lambda) < 0$.

Next, let $Q_1(d) = B^2 - D^2 F^2$ and $Q_2(d) = A^2 - 2B - D^2$. Then (2.10) becomes

$$v^4 + Q_2(d)v^2 + Q_1(d) = 0. \tag{A.1}$$

Moreover,

$$Q_1(0) = \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} \right)^2 4(\alpha e^{-\gamma\tau})^2 - (\alpha e^{-\gamma\tau})^2 \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} \right)^2$$

$$= 3 \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau} \right)^2 (\alpha e^{-\gamma\tau})^2 > 0$$

and

$$\begin{aligned}
 Q_2(0) &= \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau}\right)^2 + 4\alpha e^{-\gamma\tau} \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau}\right) \\
 &\quad + 4(\alpha e^{-\gamma\tau})^2 - 4\alpha \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau}\right) e^{-\gamma\tau} - (\alpha e^{-\gamma\tau})^2 \\
 &= \left(\gamma + c \frac{\alpha}{\beta} e^{-\gamma\tau}\right)^2 + 3(\alpha e^{-\gamma\tau})^2 > 0.
 \end{aligned}$$

Since $Q_1(d)$ and $Q_2(d)$ depend continuously on d , we can find a constant $d_0 > 0$, depending on α, β, c, γ and τ , such that $Q_1(d) > 0$ and $Q_2(d) > 0$ for $0 \leq d < d_0$. This implies that (A.1) has no real solution v . As a result, the characteristic equation (2.6) has no purely imaginary root whenever $0 \leq d < d_0$. On the other hand, we have shown that if $d = 0$, then all solutions of (2.6) have negative real parts. Hence, all solutions of (2.6) have negative real parts, provided $0 \leq d < d_0$. \square

In order to prove Theorem 2.3, we need several technical lemmas.

Lemma A.1. *Assume that $\tau < \ln(3)/\gamma$. If $d > \max\{d_1, d_2\}$, then (2.10) (at $\tilde{E} = E^*$) has a unique positive solution $v = v(d)$, where*

$$d_1 = \frac{3\alpha c e^{-\gamma\tau} - \beta\gamma}{(3e^{-\gamma\tau} - 1)\alpha}, \quad d_2 = \frac{-M + \sqrt{M^2 + 4PG}}{2P},$$

$$P = \alpha^2(1 - e^{-\gamma\tau})(3e^{-\gamma\tau} - 1),$$

$$M = \alpha(\alpha c e^{-\gamma\tau} - \beta\gamma)(3e^{-\gamma\tau} - 1) - \alpha(3\alpha c e^{-\gamma\tau} - \beta\gamma)(1 - e^{-\gamma\tau}),$$

$$G = 4\alpha\beta\gamma c e^{-\gamma\tau} + 3(\alpha c e^{-\gamma\tau})^2 + \beta^2\gamma^2.$$

Proof. Using the second equation of (2.2), we get (at $\tilde{E} = E^*$)

$$\begin{aligned}
 B &= (\gamma + cy^*)(2\beta y^* - \beta y^* + \alpha e^{-\gamma\tau}) + y^*(-\alpha d + c\beta y^* - \alpha c e^{-\gamma\tau}) \\
 &= \gamma\alpha e^{-\gamma\tau} + (\beta\gamma - \alpha d)y^* - 2\beta c y^{*2}.
 \end{aligned}$$

Therefore, from (2.3), it follows that

$$\begin{aligned}
 B &= \gamma\alpha e^{-\gamma\tau} + (\beta\gamma - \alpha d)y^* + 2\gamma\alpha e^{-\gamma\tau} + 2[c\alpha e^{-\gamma\tau} - \beta\gamma + d\alpha(1 - e^{-\gamma\tau})]y^* \\
 &= 3\gamma\alpha e^{-\gamma\tau} + [\alpha d - \beta\gamma + 2\alpha e^{-\gamma\tau}(c - d)]y^{*2}.
 \end{aligned}$$

This implies that

$$B - DF = 2\alpha\gamma e^{-\gamma\tau} + [\alpha d(1 - e^{-\gamma\tau}) + \alpha c e^{-\gamma\tau} - \beta\gamma]y^*$$

and

$$B + DF = 4\alpha\gamma e^{-\gamma\tau} + [\alpha d(1 - 3e^{-\gamma\tau}) + 3\alpha c e^{-\gamma\tau} - \beta\gamma]y^*.$$

Using the second equation in (2.4) and the second equation in (2.2), we get

$$\begin{aligned}
 B - DF &= 2\alpha\gamma e^{-\gamma\tau} + (\beta y^* - \alpha e^{-\gamma\tau})(\gamma + cy^*) + (\alpha ce^{-\gamma\tau} - \beta\gamma)y^* \\
 &= \beta cy^{*2} + \alpha\gamma e^{-\gamma\tau} > 0.
 \end{aligned}$$

Moreover, since $\tau < \ln(3)/\gamma$, we have $3e^{-\gamma\tau} > 1$. Therefore, if $d > d_1$, then

$$\alpha d(1 - 3e^{-\gamma\tau}) + 3\alpha ce^{-\gamma\tau} - \beta\gamma < 0.$$

This shows that, provided $d > d_1$, $B + DF < 0$ if and only if

$$y^* > \frac{4\alpha\gamma e^{-\gamma\tau}}{\alpha d(3e^{-\gamma\tau} - 1) + \beta\gamma - 3\alpha ce^{-\gamma\tau}}.$$

That is, by (2.4), $B + DF < 0$ if and only if

$$\theta + \sqrt{\theta^2 + \frac{4\alpha\gamma}{\beta c} e^{-\gamma\tau}} > \frac{8\alpha\gamma e^{-\gamma\tau}}{\alpha d(3e^{-\gamma\tau} - 1) + \beta\gamma - 3\alpha ce^{-\gamma\tau}}. \tag{A.2}$$

We note that if $d > d_1$, then d_2 is real and positive. We now claim that if $d \geq d_2$, then

$$\frac{8\alpha\gamma e^{-\gamma\tau}}{\alpha d(3e^{-\gamma\tau} - 1) + \beta\gamma - 3\alpha ce^{-\gamma\tau}} \leq \theta,$$

so that (A.2) is satisfied. In fact, by (2.5),

$$\frac{8\alpha\gamma e^{-\gamma\tau}}{\alpha d(3e^{-\gamma\tau} - 1) + \beta\gamma - 3\alpha ce^{-\gamma\tau}} \leq \theta$$

if and only if

$$\frac{8\alpha\gamma e^{-\gamma\tau}}{\alpha d(3e^{-\gamma\tau} - 1) + \beta\gamma - 3\alpha ce^{-\gamma\tau}} \leq \frac{1}{\beta c} [\alpha ce^{-\gamma\tau} - \beta\gamma + \alpha d(1 - e^{-\gamma\tau})],$$

which is equivalent to (under the assumption $d > d_1$)

$$\begin{aligned}
 &\alpha^2(1 - e^{-\gamma\tau})(3e^{-\gamma\tau} - 1)d^2 \\
 &+ [\alpha(3e^{-\gamma\tau} - 1)(\alpha ce^{-\gamma\tau} - \beta\gamma) - \alpha(3\alpha ce^{-\gamma\tau} - \beta\gamma)(1 - e^{-\gamma\tau})]d \\
 &- 8\alpha\beta\gamma ce^{-\gamma\tau} - (3\alpha ce^{-\gamma\tau} - \beta\gamma)(\alpha ce^{-\gamma\tau} - \beta\gamma) \geq 0,
 \end{aligned}$$

that is, $Pd_2 + Md - G \geq 0$. Therefore, if $d \geq d_2$, (A.2) holds.

Hence, we have shown that if $d > \max\{d_1, d_2\}$, then $B - DF > 0$ and $B + DF < 0$. Thus, $B^2 - D^2F^2 < 0$ and (2.10) has a unique positive solution $v = v(d)$. \square

Lemma A.2. Assume that $\tau < \ln(2)/\gamma$. Then for sufficiently large k , there exists $d_k = 2k\pi/(\delta\tau) + o(k)$ such that the characteristic equation (2.6) has a pair of purely imaginary roots $\pm i\delta d_k$, where δ was defined in (2.12).

Proof. First of all, we consider the asymptotic form of $v = v(d)$ as $d \rightarrow \infty$. By a direct computation using (2.4), (2.5), (2.7) and (2.10), we have

$$\begin{aligned} y^* &= \frac{\alpha}{\beta c} (1 - e^{-\gamma\tau})d + o(d), & x^* &= \frac{\alpha}{c} (1 - e^{-\gamma\tau}) + o(1), \\ A &= \frac{\alpha}{\beta c} (\beta + c)(1 - e^{-\gamma\tau})d + o(d), \\ B &= \frac{\alpha^2}{\beta c} (1 - e^{-\gamma\tau})(1 - 2e^{-\gamma\tau})d^2 + o(d^2), \\ F &= -\frac{\alpha}{\beta c} (1 - e^{-\gamma\tau})d^2 + o(d^2), \end{aligned} \tag{A.3}$$

$$B^2 - D^2 F^2 = -\frac{\alpha^4}{(\beta c)^2} (1 - e^{-\gamma\tau})^3 (3e^{-\gamma\tau} - 1)d^4 + o(d^4),$$

$$A^2 - 2B - D^2 = \frac{\alpha^2}{(\beta c)^2} (1 - e^{-\gamma\tau}) [(\beta + c)^2 (1 - e^{-\gamma\tau}) + 2\beta c (2e^{-\gamma\tau} - 1)] d^2 + o(d^2),$$

$$v^2 = -\frac{1}{2} \left\{ (A^2 - 2B - D^2) - \sqrt{(A^2 - 2B - D^2)^2 - 4(B^2 - D^2 F^2)} \right\} = \delta^2 d^2 + o(d^2).$$

Therefore,

$$v = \delta d + o(d).$$

It follows that there exists $k_1 > 0$ such that for all $k \geq k_1$, we can pick d_{1k} such that $v(d_{1k}) = 2k\pi/\tau$. Clearly, $d_{1k} = 2k\pi/(\delta\tau) + o(k)$, $\sin(v(d_{1k})\tau) = 0$ and $\cos(v(d_{1k})\tau) = 1$. If we define (cf. the second equation of (2.11))

$$Q(d) := Av(d) - D[v(d)\cos(v(d)\tau) - F \sin(v(d)\tau)],$$

then

$$\begin{aligned} Q(d_{1k}) &= Av(d_{1k}) - Dv(d_{1k}) \\ &= \frac{\alpha}{\beta c} (\beta + c)(1 - e^{-\gamma\tau})\delta d_{1k}^2 - \alpha e^{-\gamma\tau} \delta d_{1k} + o(k) > 0, \end{aligned}$$

for k sufficiently large. Similarly, there exists $k_2 > 0$ such that for all $k \geq k_2$, we can find d_{2k} such that $v(d_{2k}) = 2k\pi/\tau + \pi/(2\tau)$. Therefore, $d_{2k} = 2k\pi/(\tau\delta) + o(k)$, $\sin(v(d_{2k})\tau) = 1$, $\cos(v(d_{2k})\tau) = 0$ and

$$\begin{aligned} Q(d_{2k}) &= Av(d_{2k}) + DF \\ &= \frac{\alpha}{\beta c} (\beta + c)(1 - e^{-\gamma\tau})\delta d_{2k}^2 + \alpha e^{-\gamma\tau} \left[-\frac{\alpha}{\beta c} (1 - e^{-\gamma\tau})d_{2k}^2 \right] + o(k^2) \\ &= \frac{\alpha}{\beta c} (\beta + c)(1 - e^{-\gamma\tau}) \left(\delta - \frac{\alpha e^{-\gamma\tau}}{\beta + c} \right) d_{2k}^2 + o(k^2) < 0, \end{aligned}$$

for k sufficiently large, since, by (2.12),

$$\begin{aligned} 2\delta^2 &= \frac{\alpha^2}{(\beta c)^2} (1 - e^{-\gamma\tau}) 4(\beta c)^2 (1 - e^{-\gamma\tau}) (3e^{-\gamma\tau} - 1) \\ &\quad \times \left\{ \sqrt{[(\beta + c)^2 (1 - e^{-\gamma\tau}) + 2\beta c(2e^{-\gamma\tau} - 1)]^2 + 4(\beta c)^2 (1 - e^{-\gamma\tau}) (3e^{-\gamma\tau} - 1)} \right. \\ &\quad \left. + [(\beta + c)^2 (1 - e^{-\gamma\tau}) + 2\beta c(2e^{-\gamma\tau} - 1)] \right\}^{-1} \\ &\leq \frac{\alpha^2}{(\beta c)^2} (1 - e^{-\gamma\tau}) \frac{2(\beta c)^2 (1 - e^{-\gamma\tau}) (3e^{-\gamma\tau} - 1)}{(\beta + c)^2 (1 - e^{-\gamma\tau}) + 2\beta c(2e^{-\gamma\tau} - 1)} \\ &\leq \frac{2\alpha^2}{(\beta + c)^2} (1 - e^{-\gamma\tau}) (3e^{-\gamma\tau} - 1) \leq \frac{2\alpha^2 e^{-\gamma\tau}}{(\beta + c)^2}, \end{aligned}$$

that is,

$$\delta < \frac{\alpha e^{-\gamma\tau}}{\beta + c}.$$

Since $Q(d)$ is continuous in d , there exists $d_k \in (d_{1k}, d_{2k})$ such that $Q(d_k) = 0$. Thus, for $d = d_k$, $\pm iv(d_k)$ is a pair of purely imaginary roots of (2.6). \square

Lemma A.3. Let $\lambda(d_k) = u(d_k) + iv(d_k)$ be a solution of (2.6) such that $u(d_k) = 0$ and $v(d_k) = \delta d_k + o(k)$, as given in Lemma A.2. Then $u'(d_k) \neq 0$ for sufficiently large k . Here $'$ denotes differentiation with respect to d .

Proof. By way of contradiction, we suppose that $u'(d_k) = 0$. By differentiating the first equation of (2.8) with respect to d , we get

$$\begin{aligned} -2uv' + B' &= D[F' \cos(v\tau) - v'\tau F \sin(v\tau) + v' \sin(v\tau) + vv'\tau \cos(v\tau)] \\ &= D\left[F' \cos(v\tau) + v' \sin(v\tau) + v'\tau \frac{Av}{D}\right] \\ &= D[F' \cos(v\tau) + v' \sin(v\tau)] + v'\tau Av \end{aligned}$$

at $d = d_k$. Similarly, by differentiating the second equation of (2.8), we obtain

$$\begin{aligned} A'v + Av' &= D[v' \cos(v\tau) - vv'\tau \sin(v\tau) - F' \sin(v\tau) - Fv'\tau \cos(v\tau)] \\ &= D\left[v' \cos(v\tau) - F' \sin(v\tau) - v'\tau \frac{B - v^2}{D}\right] \\ &= D[v' \cos(v\tau) - F' \sin(v\tau)] + (v^2 - B)v'\tau \end{aligned}$$

at $d = d_k$. Therefore,

$$\begin{cases} [2v + Av\tau + D \sin(v\tau)]v' = B' - DF' \cos(v\tau), \\ [A - D \cos(v\tau) - (v^2 - B)\tau]v' = -DF' \sin(v\tau) - A'v, \end{cases}$$

from which it follows that

$$\frac{A - D \cos(v\tau) - (v^2 - B)\tau}{2v + Av\tau + D \sin(v\tau)} = \frac{DF' \sin(v\tau) + A'v}{DF' \cos(v\tau) - B'}. \tag{A.4}$$

On the other hand, from (2.9), we obtained

$$\cos(v\tau) = \frac{F(B - v^2) + Av^2}{D[F^2 + v^2]}, \quad \sin(v\tau) = \frac{v(B - v^2) - FA v}{D(F^2 + v^2)}.$$

Therefore, as $d \rightarrow \infty$, we get

$$\begin{aligned} \sin(v\tau) &= -\frac{FAv}{DF^2} + o(1) = -\frac{Av}{DF} + o(1) \\ &= \frac{-\alpha(\beta + c)(1 - e^{-\gamma\tau})\delta/(\beta c)}{-\alpha e^{-\gamma\tau}\alpha(1 - e^{-\gamma\tau})/(\beta c)} + o(1) = \frac{(\beta + c)\delta}{\alpha e^{-\gamma\tau}} + o(1) \end{aligned}$$

and

$$\begin{aligned} \cos(v\tau) &= \frac{F(B - v^2)}{DF^2} + o(1) = \frac{B - v^2}{DF} + o(1) \\ &= \frac{\alpha^2(1 - e^{-\gamma\tau})(1 - 2e^{-\gamma\tau})/(\beta c) - \delta^2}{\alpha e^{-\gamma\tau}[-\alpha(1 - e^{-\gamma\tau})/(\beta c)]} + o(1) \\ &= \frac{\delta^2 + (2e^{-\gamma\tau} - 1)(1 - e^{-\gamma\tau})\alpha^2/(\beta c)}{\alpha^2 e^{-\gamma\tau}(1 - e^{-\gamma\tau})/(\beta c)} + o(1). \end{aligned}$$

Noticing that

$$A' = \frac{\alpha}{\beta c}(\beta + c)(1 - e^{-\gamma\tau}) + o(1),$$

$$B' = \frac{2\alpha^2}{\beta c}(1 - e^{-\gamma\tau})(1 - 2e^{-\gamma\tau})d + o(d),$$

$$F' = -\frac{2\alpha}{\beta c}(1 - e^{-\gamma\tau})d + o(d),$$

we have that the right-hand side of (A.4) equals

$$\begin{aligned} & \alpha e^{-\gamma\tau} \left[-\frac{2\alpha}{\beta c} (1 - e^{-\gamma\tau}) d \right] \frac{(\beta + c)\delta}{\alpha e^{-\gamma\tau}} + \frac{\alpha}{\beta c} (\beta + c)(1 - e^{-\gamma\tau})\delta d + o(d) \\ & \times \left\{ -\alpha e^{-\gamma\tau} \frac{2\alpha}{\beta c} (1 - e^{-\gamma\tau}) d \frac{\delta^2 + (2e^{-\gamma\tau} - 1)(1 - e^{-\gamma\tau})\alpha^2 / (\beta c)}{\alpha^2 e^{-\gamma\tau} (1 - e^{-\gamma\tau}) / (\beta c)} \right. \\ & \quad \left. - \frac{2\alpha^2}{\beta c} (1 - e^{-\gamma\tau})(1 - 2e^{-\gamma\tau})d + o(d) \right\}^{-1} \\ & = \frac{(\beta + c)\alpha(1 - e^{-\gamma\tau})}{2\delta\beta c} + o(1) > 0 \end{aligned}$$

and the left-hand side of (A.4) equals

$$-\frac{(v^2 - B)\tau}{Av\tau} + o(1) = \frac{B - v^2}{Av} + o(1) = \frac{-(2e^{-\gamma\tau} - 1)(1 - e^{-\gamma\tau})\alpha^2 / (\beta c) - \delta^2}{\alpha(\beta + c)(1 - e^{-\gamma\tau})\delta / (\beta c)} + o(1) < 0.$$

This is contrary to (A.4). Therefore, $u'(d_k) \neq 0$. \square

Proof of Theorem 2.3. With the above technical lemmas, Theorem 2.3 is an immediate consequence of the Hopf bifurcation theorem for retarded functional differential equations developed by Nussbaum [12,13] (see also [2,5]). \square

Appendix B. Proofs of the main results in Section 3

Proof of Theorem 3.1. Let (x^*, y^*) be a positive equilibrium of (3.1). Since $y^* > 0$, from the second equation of (3.2) we obtain

$$x^* = \frac{\beta}{d} y^* - \frac{\alpha e^{-\gamma\tau}}{d}. \tag{B.1}$$

Subtracting the product of the second equation of (3.2) with cy^* from the product of the first equation of (3.2) with d , we get

$$-\gamma dx^* - \alpha de^{-\gamma\tau} y^* + \alpha dy^* - \alpha ce^{-\gamma\tau} y^* + \beta cy^{*2} = 0.$$

It follows that

$$x^* = \frac{\beta c}{\gamma d} \left[y^{*2} + \left(\frac{\alpha d(1 - e^{-\gamma\tau})}{\beta c} - \frac{\alpha e^{-\gamma\tau}}{\beta} \right) y^* \right]. \tag{B.2}$$

Let Γ_1 (respectively Γ_2) denote the graphs of (B.2) (respectively (B.1)) on the y^*-x^* -plane. Then Γ_1 is a parabola and Γ_2 is a straight line. We are interested in the points of intersection (there are at most two) of Γ_1 and Γ_2 in the first quadrant.

Clearly, Γ_2 intersects the y^* -axis at $(\alpha e^{-\gamma\tau}/\beta, 0)$. By equating the x^* from (B.1) and (B.2), we get

$$\frac{\beta}{d}y^* - \frac{\alpha e^{-\gamma\tau}}{d} = \frac{\beta c}{\gamma d} \left[y^{*2} + \left(\frac{\alpha d(1 - e^{-\gamma\tau})}{\beta c} - \frac{\alpha e^{-\gamma\tau}}{\beta} \right) y^* \right],$$

that is,

$$y^{*2} - ay^* + \frac{\alpha\gamma}{\beta c} e^{-\gamma\tau} = 0, \tag{B.3}$$

where

$$a = \frac{\gamma}{c} + \frac{\alpha}{\beta c} (c + d) e^{-\gamma\tau} - \frac{\alpha d}{\beta c}.$$

We can solve (B.3) and obtain the two roots

$$y^* = \frac{1}{2} [a \pm \sqrt{\Delta}],$$

where Δ is the discriminant, given by

$$\Delta = a^2 - \frac{4\alpha\gamma}{\beta c} e^{-\gamma\tau} = p \left(p + 4\sqrt{\frac{\alpha\gamma}{\beta c} e^{-\gamma\tau}} \right) = p \left(a + 2\sqrt{\frac{\alpha\gamma}{\beta c} e^{-\gamma\tau}} \right),$$

since $p = a - 2\{\alpha\gamma e^{-\gamma\tau}/(\beta c)\}^{1/2}$.

Clearly a positive equilibrium for (3.1) corresponds to a root $y^* = k$ of (B.3) with $k > \alpha e^{-\gamma\tau}/\beta$.

If $p < 0$ and $a \geq 0$, then $\Delta < 0$ and (B.3) has no real root. If $p < 0$ and $a < 0$, then any real root of (B.3) must be nonpositive. Hence, in any case, (3.1) has no positive equilibrium, provided $p < 0$.

Next we consider the case when $p > 0$. In that case, $\Delta > 0$ and (B.3) has two real solutions

$$y_1^* = \frac{1}{2}q_1, \quad y_2^* = \frac{1}{2}q_2,$$

where q_1 and q_2 were defined in (3.3). The corresponding x^* 's are given by:

$$x_1^* = \frac{\beta}{2d} \left(q_1 - \frac{2\alpha}{\beta} e^{-\gamma\tau} \right), \quad x_2^* = \frac{\beta}{2d} \left(q_2 - \frac{2\alpha}{\beta} e^{-\gamma\tau} \right).$$

Clearly, $q_2 > q_1$. Therefore, if $q_1 > 2\alpha e^{-\gamma\tau}/\beta$, then $x_1^*, x_2^* > 0$. Consequently, (3.1) has two positive equilibria (x_1^*, y_1^*) and (x_2^*, y_2^*) .

On the other hand, if $q_1 \leq 2\alpha e^{-\gamma\tau}/\beta$, then $x_1^* \leq 0$; so that (x_1^*, y_1^*) is not a positive equilibrium for (3.1). Therefore, if in addition $q_2 > 2\alpha e^{-\gamma\tau}/\beta$, then (3.1) has a unique positive equilibrium, namely, (x_2^*, y_2^*) . Similarly, if $q_2 \leq 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has no positive equilibrium.

Finally, in the case $p = 0$, $q_1 = q_2 = 2\{\alpha\gamma e^{-\gamma\tau}/(\beta c)\}^{1/2}$. Therefore, if $q_1 > 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has a unique positive equilibrium. But if $q_1 \leq 2\alpha e^{-\gamma\tau}/\beta$, (3.1) has no positive equilibrium. \square

Proof of Theorem 3.3. If $\beta\gamma \neq \alpha c$ and $\tau = 0$, then

$$p = \frac{\beta\gamma + \alpha c - 2\sqrt{\alpha\gamma\beta c}}{\beta c} = \frac{(\sqrt{\beta\gamma} - \sqrt{\alpha c})^2}{\beta c} > 0, \quad (\text{B.4})$$

$$q_1 = \frac{\beta\gamma + \alpha c}{\beta c} - \frac{|\beta\gamma - \alpha c|}{\beta c}, \quad q_2 = \frac{\beta\gamma + \alpha c}{\beta c} + \frac{|\beta\gamma - \alpha c|}{\beta c}.$$

Therefore, if $\beta\gamma > \alpha c$, then $q_1 = 2\alpha/\beta < q_2 = 2\gamma/c$. By Theorem 3.1, (3.1) has one positive equilibrium. Similarly, if $\beta\gamma < \alpha c$, then $q_1 = 2\gamma/c < 2\alpha/\beta = q_2$. Again, by Theorem 3.1, (3.1) has no positive equilibrium.

Next,

$$\begin{aligned} \frac{d}{d\tau} p \Big|_{\tau=0} &= -\frac{\alpha\gamma}{\beta c} (c+d) + \gamma \sqrt{\frac{\alpha\gamma}{\beta c}}, \\ \frac{d}{d\tau} q_1 \Big|_{\tau=0} &= p' - \gamma \sqrt{\frac{\alpha\gamma}{\beta c}} - \frac{2pp' + 4p'\sqrt{\alpha\gamma/(\beta c)} - 2p\gamma\sqrt{\alpha\gamma/(\beta c)}}{2\sqrt{p(p + 4\sqrt{\alpha\gamma/(\beta c)})}} \\ &= -\frac{\alpha\gamma}{\beta c} (c+d) - \frac{(\beta\gamma + \alpha c)p' / (\beta c) - p\gamma\sqrt{\alpha\gamma/(\beta c)}}{|\beta\gamma - \alpha c| / (\beta c)} \\ &= -\frac{\alpha\gamma}{\beta c} (c+d) - \frac{(\beta\gamma + \alpha c)p' - p\gamma\sqrt{\alpha\gamma\beta c}}{|\beta\gamma - \alpha c|} \\ &= -\frac{\alpha\gamma}{\beta c} (c+d) - \frac{\gamma}{|\beta\gamma - \alpha c|} \left[(\beta\gamma + \alpha c) \left(\sqrt{\frac{\alpha\gamma}{\beta c}} - \frac{\alpha}{\beta c} (c+d) \right) - p\sqrt{\alpha\gamma\beta c} \right]. \end{aligned}$$

If $\beta\gamma > \alpha c$, then

$$\begin{aligned} \frac{d}{d\tau} q_1 \Big|_{\tau=0} &= -\frac{\alpha\gamma}{\beta c} (c+d) + \frac{\gamma}{\beta\gamma - \alpha c} \frac{\alpha}{\beta c} (c+d)(\beta\gamma + \alpha c) \\ &\quad - \frac{\gamma}{\beta\gamma - \alpha c} \left[(\beta\gamma + \alpha c) \sqrt{\frac{\alpha\gamma}{\beta c}} - p\sqrt{\alpha\gamma\beta c} \right] \\ &= \frac{2\alpha\gamma}{\beta\gamma - \alpha c} \frac{\alpha\gamma}{\beta c} (c+d) - \frac{\gamma}{\beta\gamma - \alpha c} \left[\frac{\beta\gamma + \alpha c}{\beta c} - p \right] \sqrt{\alpha\gamma\beta c} \\ &= \frac{2\alpha^2\gamma}{\beta(\beta\gamma - \alpha c)} (c+d) - \frac{2\alpha\gamma^2}{\beta\gamma - \alpha c}, \end{aligned}$$

so that

$$\begin{aligned} e^{-\gamma\tau} \frac{d}{d\tau} (e^{\gamma\tau} q_1) \Big|_{\tau=0} &= \gamma q_1 \Big|_{\tau=0} + \frac{d}{d\tau} q_1 \Big|_{\tau=0} \\ &= \frac{2\alpha\gamma}{\beta} + \frac{2\alpha^2\gamma}{\beta(\beta\gamma - \alpha c)} (c+d) - \frac{2\alpha\gamma^2}{\beta\gamma - \alpha c} = \frac{2\alpha^2\gamma d}{\beta(\beta\gamma - \alpha c)} > 0. \end{aligned}$$

Hence, if $\tau > 0$ is sufficiently small, we have

$$e^{\gamma\tau}q_1 > q_1|_{\tau=0} = \frac{2\alpha}{\beta},$$

that is,

$$q_1 > \frac{2\alpha}{\beta} e^{-\gamma\tau}.$$

Therefore, by Theorem 3.1, (3.1) has two positive equilibria.

If $\beta\gamma < \alpha c$, we can similarly show that

$$e^{-\gamma\tau} \frac{d}{d\tau} (e^{\gamma\tau}q_2) \Big|_{\tau=0} = \frac{2\alpha^2\gamma d}{\beta(\beta\gamma - \alpha c)} < 0.$$

Again, by Theorem 3.1, (3.1) has no positive equilibrium. \square

Proof of Theorem 3.5. Let $f(\lambda)$ denote the left-hand side of (3.5) evaluated at $\tilde{E} = E_2$. Then $f(\infty) = \infty$ and

$$f(0) = (cy_2^* - \gamma)(dx_2^* - 2\beta y_2^*) - dy_2^*(\alpha + cx_2^*) - \alpha e^{-\gamma\tau}(\gamma - cy_2^* - dy_2^*).$$

Recall that

$$dx_2^* = \beta y_2^* - \alpha e^{-\gamma\tau}$$

by (3.2); therefore,

$$\begin{aligned} f(0) &= [cy_2^* - \gamma][-\beta y_2^* - \alpha e^{-\gamma\tau}] - dy_2^* \left[\alpha + \frac{\beta c}{d} y_2^* - \frac{\alpha c}{d} e^{-\gamma\tau} \right] - \alpha e^{-\gamma\tau} [\gamma - cy_2^* - dy_2^*] \\ &= -2\beta cy_2^{*2} + y_2^* [\beta\gamma - \alpha d + \alpha(c+d)e^{-\gamma\tau}] \\ &= -2\beta cy_2^* \left[y_2^* - \frac{1}{2} \left(\frac{\gamma}{c} - \frac{\alpha d}{\beta c} + \frac{\alpha(c+d)}{\beta c} e^{-\gamma\tau} \right) \right] \\ &= -2\beta cy_2^* \left[y_2^* - \frac{1}{2}a \right]. \end{aligned}$$

Since y_2^* is the larger root of (B.3), $y_2^* > \frac{1}{2}a$ and hence $f(0) < 0$. Therefore, there exists $\lambda_0 > 0$ such that $f(\lambda_0) = 0$. This implies that the characteristic equation (3.5) has a positive root and therefore E_2 is unstable. \square

Proof of Theorem 3.6. The characteristic equation (3.5) evaluated at $\tilde{E} = E_1$ can be rewritten as

$$\lambda^2 + A\lambda + B + (C\lambda + D)e^{-\gamma\tau} = 0,$$

where

$$\begin{aligned} A &= 2\beta y_1^* + \gamma - cy_1^* - dx_1^* = (\beta - c)y_1^* + \gamma + \alpha e^{-\gamma\tau}, \\ B &= [cy_1^* - \gamma][dx_1^* - 2\beta y_1^*] - dy_1^*[\alpha + cx_1^*] = (\beta\gamma - \alpha d)y_1^* - 2\beta cy_1^{*2} + \alpha\gamma e^{-\gamma\tau}, \\ C &= -\alpha e^{-\gamma\tau}, \quad D = -\alpha e^{-\gamma\tau}[\gamma - (c+d)y_1^*]. \end{aligned}$$

We also note that

$$y_1^* = \frac{1}{2} \left(a - \sqrt{a^2 - \frac{4\alpha\gamma}{\beta c} e^{-\gamma\tau}} \right) = \frac{2\alpha\gamma e^{-\gamma\tau}/(\beta c)}{a + \sqrt{a^2 - 4\alpha\gamma e^{-\gamma\tau}/(\beta c)}}.$$

Thus, we have the following asymptotic expressions:

$$a = \frac{\beta\gamma - \alpha d}{\beta c} + \frac{\alpha}{\beta c} (c + d)e^{-\gamma\tau} = \frac{\beta\gamma - \alpha d}{\beta c} + O(e^{-\gamma\tau}),$$

$$y_1^* = \frac{\alpha\gamma}{\beta\gamma - \alpha d} e^{-\gamma\tau} + o(e^{-\gamma\tau})$$

and

$$\begin{aligned} A &= \gamma + O(e^{-\gamma\tau}), & B &= 2\alpha\gamma e^{-\gamma\tau} + o(e^{-\gamma\tau}), \\ C &= -\alpha e^{-\gamma\tau}, & D &= -\alpha\gamma e^{-\gamma\tau} + o(e^{-\gamma\tau}). \end{aligned}$$

Therefore, if τ is sufficiently large, we have

$$\begin{aligned} A &> 0, & B &> 0, \\ B^2 - D^2 &= 3(\alpha\gamma e^{-\gamma\tau})^2 + o(e^{-2\gamma\tau}) > 0, \\ AB - CD &= 2\alpha\gamma^2 c^{-\gamma\tau} + o(e^{-\gamma\tau}) > 0, \\ A^2 - C^2 - 2B &= \gamma^2 + o(1) > 0. \end{aligned}$$

Therefore, by a result in [3], all roots of (3.5) have negative real parts. Consequently, E_1 is asymptotically stable. \square

Proof of Theorem 3.7. Since $\beta\gamma > \alpha c$, by Theorem 3.3, (3.1) has two positive equilibria: E_1 and E_2 . E_2 is always unstable by Theorem 3.5. It remains to show that E_1 is asymptotically stable. As in the proof of Theorem 3.6, the characteristic equation (3.5) at E_1 can be written as

$$\lambda^2 + A\lambda + B + (C\lambda + D)e^{-\gamma\tau} = 0,$$

where

$$\begin{aligned} A &= (\beta - c)y_1^* + \gamma + \alpha e^{-\gamma\tau}, & B &= (\beta\gamma - \alpha d)y_1^* - 2\beta c y_1^{*2} + \alpha\gamma e^{-\gamma\tau}, \\ C &= -\alpha e^{-\gamma\tau}, & D &= -\alpha e^{-\gamma\tau} [\gamma - (c + d)y_1^*]. \end{aligned}$$

Note that by (B.4), as $\tau \rightarrow 0^+$,

$$y_1^* = \frac{1}{2}q_1 = \frac{\alpha}{\beta} + o(1),$$

so that

$$\begin{aligned} A &= 2\alpha + \frac{\beta\gamma - \alpha c}{\beta} + o(1) > 0, & B &= \frac{2\alpha}{\beta} [\beta\gamma - \alpha(c + \frac{1}{2}d)] + o(1) > 0, \\ C &= -\alpha + o(1), & D &= -\frac{\alpha}{\beta} [\beta\gamma - \alpha(c + d)] + o(1). \end{aligned}$$

Consequently,

$$\begin{aligned}
 B^2 - D^2 &= \frac{\alpha^2}{\beta^2} [2\beta\gamma - 2\alpha(c + \frac{1}{2}d) + \beta\gamma - \alpha(c + d)] \\
 &\quad \times [2\beta\gamma - 2\alpha(c + \frac{1}{2}d) - \beta\gamma + \alpha(c + d)] + o(1) \\
 &= \frac{3\alpha^2}{\beta^2} [\beta\gamma - \alpha(c + \frac{2}{3}d)] [\beta\gamma - \alpha c] + o(1) > 0, \\
 AB - CD &= \left(2\alpha + \frac{\beta\gamma - \alpha c}{\beta}\right) \frac{2\alpha}{\beta} [\beta\gamma - \alpha(c + \frac{1}{2}d)] - \frac{\alpha^2}{\beta} [\beta\gamma - \alpha(c + d)] + o(1) \\
 &> \frac{\alpha^2}{\beta} [4\beta\gamma - 4\alpha(c + \frac{1}{2}d) - \beta\gamma + \alpha(c + d)] + o(1) \\
 &= \frac{3\alpha^2}{\beta} [\beta\gamma - \alpha(c + \frac{1}{3}d)] + o(1) > 0
 \end{aligned}$$

and

$$\begin{aligned}
 A^2 - C^2 - 2B &= \left[2\alpha + \frac{\beta\gamma - \alpha c}{\beta}\right]^2 - \alpha^2 - \frac{4\alpha}{\beta} [\beta\gamma - \alpha c - \frac{1}{2}\alpha d] + o(1) \\
 &> \frac{4\alpha}{\beta} [\beta\gamma - \alpha c - \beta\gamma + \alpha c + \frac{1}{2}\alpha d] + o(1) > 0.
 \end{aligned}$$

Therefore, again by a result in [3], all roots of (3.5) have negative real parts and E_1 is asymptotically stable. \square

References

- [1] W.G. Aiello and H.I. Freedman, A time-delay model of single-species growth with stage structure, *Math. Biosci.* **101** (1990) 139–153.
- [2] S.N. Chow, J. Mallet-Paret and J.A. Yorke, Global Hopf bifurcation from a multiple eigenvalue, *Nonlinear Anal.* **2** (1978) 753–763.
- [3] J. Chuma and P. van den Driessche, A general second-order transcendental equation, *Appl. Math. Notes* **5** (1980) 85–96.
- [4] O. Diekmann, R.M. Nisbet, W.S.C. Gurney and F. van den Bosch, Simple mathematical models for cannibalism: a critique and a new approach, *Math. Biosci.* **78** (1986) 21–46.
- [5] L.H. Erbe, K. Gęba, W. Krawcewicz and J. Wu, S^1 -degree and global Hopf bifurcation theory of functional differential equations, *J. Differential Equations* **96** (1992) 277–298.
- [6] J.C. Frauenthal, Some simple models of cannibalism, *Math. Biosci.* **63** (1983) 87–98.
- [7] H.I. Freedman and J. Wu, Persistence and global asymptotic stability of single species dispersal models with stage structure, *Quart. Appl. Math.* **49** (1991) 351–371.
- [8] B.D. Hassard, N.D. Kazarinoff and Y.-H. Wan, *Theory and Applications of Hopf Bifurcation* (Cambridge Univ. Press, Cambridge, 1981).
- [9] A. Hastings, Cycles in cannibalistic egg larval interactions, *J. Math. Biol.* **24** (1987) 651–666.

- [10] A. Hastings and R.F. Constantino, Cannibalistic egg-larval interactions in *Tribolium*: an explanation for the oscillation in larval numbers, *Amer. Nat.* **130** (1987) 36–52.
- [11] M.W. Hirsch, Stability and convergence in strongly monotone dynamical systems, *J. Reine Angew. Math.* **383** (1988) 1–53.
- [12] R.D. Nussbaum, A global bifurcation theorem with application to functional differential equations, *J. Funct. Anal.* **19** (1975) 319–338.
- [13] R.D. Nussbaum, A global Hopf bifurcation theorem for retarded functional differential equations, *Trans. Amer. Math. Soc.* **238** (1978) 139–164.
- [14] J.C. Rodriguez, Models of growth with density regulation in more than one life stage, *Theoret. Population Biol.* **34** (1988) 93–117.
- [15] H.L. Smith, Monotone semiflows generated by functional differential equations, *J. Differential Equations* **66** (1987) 420–442.