Stage-structured cannibalism with delay in maturation and harvesting of an adult predator

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Received: 5 January 2012 / Accepted: 20 August 2012 / Published online: 22 November 2012
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Abstract A three-dimensional stage-structured predator–prey model is proposed and analyzed to study the effect of predation and cannibalism of the organisms at the highest trophic level with non-constant harvesting. Time lag in maturation of the predator is introduced in the system and conditions for local asymptotic stability of steady states are derived. The length of the delay preserving the stability is also estimated. Moreover, it is shown that the system undergoes a supercritical Hopf bifurcation when the maturation time lag crosses a certain critical value. Computer simulations have been carried out to illustrate various analytical results.

Keywords Stage-structured population dynamics · Cannibalism · Maturation delay · Harvesting

1 Introduction

A stage-structured model of population growth consists of juvenile and adult organisms where juvenile organisms can neither predate nor reproduce [1]. In the real world, almost all organisms have a juvenile stage where only adult predators can attack prey and have reproductive ability [2]. Also, cannibalism is a prevalent feature of stage-structured populations in both aquatic and terrestrial food webs [3]. Intraguild predation (IGP) is an ecological interaction in which two competing species interact as predator and prey for a shared resource. Intraguild predation can be classified as symmetrical or asymmetrical [4]. Symmetric IGP occurs when there is mutual predation between two species, whereas in asymmetrical interaction, one species consistently preys upon the other. Stage-structure with cannibalism among predators competing for the same resource is asymmetric intraguild predation [5, 6].

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IGP has a strong impact on population dynamics because consumption of small predators by large conspecifics reduces the predation pressure on prey [7].

Two species, *Parrotfish* (*Scarus spp.*) and *Pterois volitans* (lionfish) are considered for the study of interactions within and among stage-structured populations. It has been observed that in the presence of predatory *Pterois volitans*, there is a rapid loss of herbivorous *Parrotfish* in coral reef ecosystems that disrupt the delicate ecological balance in which they exist, leading to coral bleaching [8–10]. According to NOAA, commercial harvesting of adult *Pterois volitans* is required to reduce the number of *Pterois volitans* to mitigate their impact on coral reef ecosystems [11, 12].

Pterois volitans occupies one of the top levels of the food web in many coral reef environments. They are known to feed mostly on small fishes, which include juveniles

Fig. 1 Schematic diagram of intraguild predation with delay

of its species [13]. The *Parrotfish* preys on algae for its growth [14, 15]. We study a stage-structured predator–prey system with *Parrotfish* at the first trophic level and *Pterois volitans* at the remaining two trophic levels (Fig. 1). More specifically, the juvenile *Pterois volitans* are at the second trophic level and the adult *Pterois volitans* are at the third trophic level. In our study, we assume that only adult *Pterois volitans* prey on *Parrotfish* and have reproductive ability. Apart from preying on *Parrotfish*, adult *Pterois volitans* exhibit a distinct cannibalistic attitude towards its juvenile species.

We have also taken into account a non-constant harvesting policy of adult *Pterois volitans* to control the growth of this invasive species [16]. We assume that the reproduction of adult *Pterois volitans* after predating *Parrotfish* is not instantaneous but will be mediated by some discrete maturation time delay required for egg deposition, embryo development, and hatching [17]. We will examine how the interactions of *Parrotfish* and juvenile and adult *Pterois volitans* determine predator–prey dynamics and the role of the harvesting policy in controlling dynamic instability of the system. We have estimated the delay for which the system preserves its stability around the positive steady state. We have also derived the conditions for instability of the system around the interior equilibrium and Hopf bifurcation. We have observed that in our model, the stability of the organism-free equilibrium does not depend on the time delay, whereas the stability of *Pterois volitans*-free equilibrium and the interior equilibrium depend on the delay. We show that when the parameter representing maturation time delay passes through a critical value, the interior equilibrium loses its stability and a Hopf bifurcation occurs. Numerical simulations under a default set of parameter values have been performed to support our analytical findings.

2 The basic model

We take a stage-structured model involving maturation time delay of a predator. *Parrotfish* are present at concentration $x(t)$ at time t . Two predators, juvenile and adult *Pterois volitans*, are introduced in the system with concentrations $y_J(t)$ and $y_A(t)$, respectively, at time t . It is assumed that adult *Pterois volitans* prey on both *Parrotfish* and juvenile *Pterois volitans*, while juvenile *Pterois volitans* do not attack *Parrotfish* and have no reproductive ability—an exhibition of stage-structured cannibalism. The parameter τ represents the delay in maturation of *Pterois volitans*. The delay $\tau > 0$ is a constant based on the assumption that the growth rate of juvenile *Pterois volitans* depends on the number of adult *Pterois volitans* and *Parrotfish* in time $(t-\tau)$. The predator y_A at the highest trophic level is harvested with a non-constant harvesting policy. In particular, for a more realistic approach, a rational harvesting function has been considered in the model that provides diminishing marginal returns to the harvesting organization [16].

We make the following assumptions in formulating the mathematical model:

- (H1) In the absence of *Pterois volitans*, the growth equation of *Parrotfish* follows logistic growth with only intra-specific competition with intrinsic growth rate r and carrying capacity K .
- (H2) We consider the predation form to follow a Holling type II functional response in which the rate of predation rises as prey density increases, but eventually becomes constant regardless of any increase in prey density.
- (H3) The death rate of juvenile *Pterois volitans* and transformation rate from juvenile to adult *Pterois volitans* are proportional to the existing juvenile population with proportionality constants D_1 and μ , respectively.

- (H4) The death rate of adult *Pterois volitans* is proportional to the existing adult population with a proportionality constant D_2 .
- (H5) Adult *Pterois volitans* (y_A) prey on *Parrotfish* (x) with uptake rate $\frac{m_1 xy_A}{a_1 + x}$ which leads to the delayed growth of new juveniles (y_J) with growth rate $\frac{e_1 m_1 x(t-\tau) y_A(t-\tau)}{a_1 + x(t-\tau)}$.
- (H6) Also, adult *Pterois volitans* (y_A) exhibit cannibalism on juveniles (y_J) with $\frac{m_2 y_J y_A}{a_2 + y_J}$ as uptake rate leading to the delayed growth of new juveniles (y_J) with growth rate $\frac{e_2 m_2 y_J(t-\tau) y_A(t-\tau)}{a_2 + y_J(t-\tau)}$. Thus, $m_2 \left(\frac{y_J y_A}{a_2 + y_J} - \frac{e_2 y_J(t-\tau) y_A(t-\tau)}{a_2 + y_J(t-\tau)} \right)$ represents the reduction in growth rate of juvenile *Pterois volitans* due to cannibalism.

The basic equations with all of the parameters are:

$$\begin{aligned} \frac{dx}{dt} &= rx \left(1 - \frac{x}{K} \right) - \frac{m_1 xy_A}{a_1 + x} \\ \frac{dy_J}{dt} &= \frac{e_1 m_1 x(t-\tau) y_A(t-\tau)}{a_1 + x(t-\tau)} + \frac{e_2 m_2 y_J(t-\tau) y_A(t-\tau)}{a_2 + y_J(t-\tau)} - (\mu + D_1) y_J - \frac{m_2 y_J y_A}{a_2 + y_J} \\ \frac{dy_A}{dt} &= \mu y_J - D_2 y_A - \frac{h y_A}{c + y_A} \end{aligned} \quad (1)$$

where $x(0) = x_0 \geq 0$, $y_J(0) = y_{J_0} \geq 0$, $y_A(0) = y_{A_0} \geq 0$.

Here, $\frac{1}{\mu}$ represents the total time spent by *Pterois volitans* in its juvenile stage; h is the maximum harvesting rate of adult *Pterois volitans* and c is the concentration of adult *Pterois volitans* for which the rate of harvesting is half its maximum. Also, m_i are the maximal growth ('birth') rates, a_i are the half saturation constants, which are the nutrient concentrations at which the functional response of the species is half maximal, and e_i are growth efficiency of juvenile and adult *Pterois volitans*, respectively ($i = 1, 2$); all of these are positive quantities [17–19]. The parameters h and c are environmental parameters, while τ , μ , m_i , a_i , D_i and e_i are properties of the organisms [20].

3 Invariance and boundedness of the system

Obviously, the right-hand sides of the equations in system (1) are continuous, non-negative smooth functions on $R_+^3 = \{(x, y_J, y_A) : x, y_J, y_A \geq 0\}$. Indeed, they are Lipschitzian on R_+^3 and so the solution of the system (1) exists and is unique. Therefore, with Theorem 3.1 it is possible to prove that the interior of the positive octant of R^3 is an invariant region.

Theorem 3.1 For large values of t , all the solutions of (1) enter into the set $\left\{ (x, y_J, y_A) \in R^3 : x(t) + y_J(t) + y_A(t) < \frac{rK}{D_0} \right\}$, where $D_0 = \min \{r, D_1, D_2\}$.

The proof is in the [Appendix](#).

4 Qualitative analysis of the model without time delay ($\tau = 0$)

In this section, we restrict ourselves to analyzing the model in the absence of delay. Thus, only the interaction parts of the model system are taken into account. In the absence of delay, the system (1) reduces to

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{m_1 xy_A}{a_1 + x} \equiv F^1 \\ \frac{dy_J}{dt} &= \frac{e_1 m_1 xy_A}{a_1 + x} - (\mu + D_1) y_J - \frac{(1 - e_2) m_2 y_J y_A}{a_2 + y_J} \equiv F^2 \\ \frac{dy_A}{dt} &= \mu y_J - D_2 y_A - \frac{h y_A}{c + y_A} \equiv F^3\end{aligned}\quad (2)$$

where $x(0) = x_0 \geq 0$, $y_J(0) = y_{J_0} \geq 0$, $y_A(0) = y_{A_0} \geq 0$.

We now study the model analytically with $\tau = 0$. The proofs are reserved for the [Appendix](#).

The system will be permanent if there exist $u_i, M_i \in (0, \infty)$ such that $u_i \leq \lim_{t \rightarrow \infty} u_i(t) \leq M_i$, for each organism $u_i(t)$ in the system [21, 22]. Permanence represents convergence on an interior attractor from any positive initial conditions, and so it can be regarded as a strong form of coexistence. From a biological point of view, permanence of a system ensures the survival of all the organisms in the long run.

Since $x(t) + y_J(t) + y_A(t) < \frac{rK}{D_0}$ as $t \rightarrow \infty$ it follows that there exist positive numbers M_1, M_2 with $M_1 + M_2 < \frac{rK}{D_0}$ such that $x(t) \leq M_1$ and $y(t) \leq M_2$ for large values of t .

The following lemma rules out the possibility of extinction of any organism in the system under suitable conditions.

Theorem 4.1 *If there exist finite positive real numbers x_1, y_{J_1}, y_{A_1} with $x_1 = K(1 - \frac{m_1 M_2}{a_1 r})$, $y_{A_1}(t) > \frac{M_1(\mu + D_2)(a_1 + x_1)}{x_1(e_1 m_1 - m_2) - a_1 m_2}$ and $r > \frac{m_1 M_2}{a_1}$, then for large values of t , each solution of the system (2) with positive initial values enters in the compact set $\{(x, y_J, y_A) : x_1 \leq x(t) \leq K, y_{J_1} \leq y_J(t) \leq M_1, y_{A_1} \leq y_A(t) \leq M_2\}$ and remains in it finally.*

The system (2) possesses the following equilibria:

- (i) organism-free equilibrium $E_0 = (0, 0, 0)$;
- (ii) *Pterois volitans*-free equilibrium $E_1 = (K, 0, 0)$;
- (iii) the equilibrium of coexistence $E^* = (x^*, y_J^*, y_A^*)$, where x^* satisfies the equation $\frac{e_1 m_1 x \theta(x)}{a_1 + x} - (\mu + D_1) \phi(x) - \frac{(1 - e_2) m_2 \theta(x) \phi(x)}{a_2 + \phi(x)} = 0$, with $y_J^* = \phi(x^*) = \frac{1}{\mu} \left(D_2 + \frac{h}{c + \theta(x^*)} \right)$ $\theta(x^*)$ and $y_A^* = \theta(x^*) = \frac{r \gamma_1 (a_1 + x^*) (K - x^*)}{m_1 K}$. If $r > \frac{m_1 M_2}{a_1}$ holds then $x^* > 0$ and consequently, $y_J^* > 0$ and $y_A^* > 0$.

System (2) is competitive [23] if there exists a diagonal matrix $H = \text{diag}(\epsilon_1, \epsilon_2, \epsilon_3)$, where ϵ_i is either 1 or -1 ($i = 1, 2, 3$), such that $HJ(X)H$ has non-positive off-diagonal elements, where $J(X)$ is the Jacobian of the system (2).

By choosing $H = \text{diag}(1, -1, 1)$ we see that all the off-diagonal elements of $HJ(X)H$ are non-positive if the following lemma is satisfied:

Lemma 4.2 *The system (2) is competitive if $r > \frac{m_1 M_2}{a_1}$ and $K \geq \frac{a_1 r \{m_2(1-e_2)(1+a_1)\}}{e m_1(a_1 r - m_1 M_2)}$.*

Lemma 4.3 *The critical point $E_0 = (0, 0, 0)$ of the system (2) is always unstable.*

Lemma 4.4 *The critical point $E_1 = (K, 0, 0)$ of the system (2) is locally asymptotically stable if $h > c \left\{ \frac{e_1 m_1 \mu K}{(a_1 + K)(\mu + D_1)} - D_2 \right\}$.*

Corollary 4.1 *If $K < \frac{a_1 D_2(\mu + D_1)}{e_1 m_1 \mu - D_2(\mu + D_1)}$, then the system is locally asymptotically stable at E_1 even in the absence of harvesting.*

The system is persistent if all the boundary equilibria repel interior trajectories [24]. The following lemma gives the condition of persistence of the system (2):

Lemma 4.5 *The system (2) is persistent at E^* if $h \leq c \left\{ \frac{e_1 m_1 \mu K}{(a_1 + K)(\mu + D_1)} - D_2 \right\}$.*

Corollary 4.2 *The system (2) is persistent at E^* in the absence of harvesting if $K \geq \frac{a_1 D_2(\mu + D_1)}{e_1 m_1 \mu - D_2(\mu + D_1)}$.*

Lemma 4.6 *The critical point E^* of the system (2) is locally asymptotically stable if $h > \frac{(c+y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1-e_1)m_2 a_2 y_A^*}{(a_2 + y_A^*)^2} - \mu - D_1 - D_2 - r \right\}$ and $\eta > 0$, where $\eta = \left\{ \mu + D_1 + D_2 + \frac{hc}{(c+y_A^*)^2} + \frac{(1-e_1)m_2 a_2 y_A^*}{(a_2 + y_A^*)^2} \right\} \times \left[\left\{ r^2 + D_2 + \frac{hc}{(c+y_A^*)^2} - \frac{m_1 r y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1-e_1)m_2 a_2 y_A^*}{(a_2 + y_A^*)^2} \right\} + \left\{ r^2 - \frac{m_1 r y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \left\{ r + D_2 + \frac{hc}{(c+y_A^*)^2} - \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} - \mu(\mu + D_1) \frac{y_A^*}{y_A^*} \right] - \frac{e_1 m_1^2 a_1 \mu x^* y_A^*}{(a_1 + x^*)^3}$.*

Suppose system (2) has a periodic solution $p(t)$ with minimal period $\omega > 0$ and orbit $\Gamma = \{p(t) : 0 \leq p(t) \leq \omega\}$. The orbital stability [25] of Γ implies that corresponding to $\epsilon > 0$, there exists $\delta > 0$ such that for any solution $u(t)$ of the system, $|u(t) - \Gamma| < \epsilon$ whenever $|u(t) - u(0)| < \delta$.

Γ is asymptotically orbitally stable if it is orbitally stable subject to the condition $u(t) \rightarrow \Gamma$ as $t \rightarrow \infty$. Also, the system (2) is said to have stable periodic orbits, if and only if the orbit of any periodic solution, if it exists, is asymptotically orbitally stable [25]. The following lemma gives the condition for stable periodic orbits of the system.

Lemma 4.7 *If the system is permanent, then the system will have stable periodic orbits.*

If the system is locally asymptotically stable at E^* and the conditions for permanence and competitiveness are satisfied, then E^* is globally asymptotically stable [26].

Lemma 4.8 *The system (2) undergoes a Hopf bifurcation at $h = h_{cr}$ iff*

- (i) $h_{cr} > \max \{h_0, h_1, h_2\}$,
- (ii) $f_1(h_{cr}) = f_2(h_{cr})$,
- (iii) $\{M(h)K(h) + N(h)L(h)\}_{h_{cr}} \neq 0$,

where $f_1(h) = A(h)B(h)$, $f_2(h) = C(h)$,

$$\begin{aligned}
 h_0 &= \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\}, \\
 h_1 &= \frac{(c + y_A^*)^2 \left[\mu (\mu + D_1) \frac{y_J^*}{y_A^*} + \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - D_2 - r \right\} \left\{ \mu + D_1 + D_2 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} + D_2^2 \right]}{c \left\{ \mu + D_1 + r + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\}}, \\
 h_2 &= \frac{(c + y_A^*)^2 (a_2 + y_J^*)^2}{c \left\{ (a_2 + y_J^*) (\mu + D_1) + (1 - e_1) m_2 a_2 y_A^* \right\}} \\
 &\quad \times \left[\left\{ \frac{e m_1^2 a \mu x^* y_A^*}{(a_1 + x^*) \left\{ r (a_1 + x^*)^2 - m_1 y_A^* (a_1 + 2x^*) \right\}} + \mu (\mu + D_1) \frac{y_J^*}{y_A^*} \right\} - D_2 \right], \\
 A &= \mu + D_1 + D_2 + r + \frac{hc}{(c + y_A^*)^2} + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2}, \\
 B &= \left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} - \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - r \right\} \\
 &\quad \times \left\{ \mu + D_1 + D_2 + \frac{(1 - e_1) m_1 a_2 y_A^*}{(a_2 + y_J^*)^2} + \frac{hc}{(c + y_A^*)^2} \right\} - \mu (\mu + D_1) \frac{y_J^*}{y_A^*}, \\
 C &= \left\{ r - \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \left[\left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \right. \\
 &\quad \times \left. \left\{ \mu + D_1 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} - \mu (\mu + D_1) \frac{y_J^*}{y_A^*} \right] - \frac{e_1 m_1^2 a_1 \mu x^* y_A^*}{(a_1 + x^*)^3},
 \end{aligned}$$

$$\begin{aligned}
 K(h) &= 3\beta_1^2(h) - 3\beta_2^2(h) + 2A(h)\beta_1(h) + B(h), \quad L(h) \\
 &= 6\beta_1(h)\beta_2(h) + 2A(h)\beta_2(h),
 \end{aligned}$$

$$\begin{aligned}
 M(h) &= C'(h) + \{\beta_1^2(h) - \beta_2(h)\} A'(h) + \beta_1 B'(h), \quad N(h) \\
 &= 2\beta_1(h)\beta_2(h) A'(h) + \beta_2(h) B'(h);
 \end{aligned}$$

$\beta_1(h)$ and $\beta_2(h)$ are real and imaginary parts, respectively, of a pair of eigenvalues in $h \in (h_{cr} - \epsilon, h_{cr} + \epsilon)$.

Corollary 4.3 The period T of the bifurcating periodic orbits close to $h = h_{cr}$ is given by

$$T(h_{cr}) = \frac{2\pi}{\sqrt{B(h_{cr})}}.$$

The condition (iii) is equivalent to $\frac{dg(h)}{dh}|_{(h=h_{cr})} \neq 0$, where $g(h) = f_1(h) - f_2(h)$.

Thus, by using numerical methods, condition (ii) can be verified by showing that the curves $y = f_1(h)$ and $y = f_2(h)$ intersect at $h = h_{cr}$, whereas the condition (iii) can be

verified by showing that the tangent to the curve $y = g(h)$ at $h = h_{cr}$ is not parallel to the h axis [27].

We investigate the orbital stability of Hopf-bifurcating periodic solution by using Poore's sufficient condition [28]. The supercritical and subcritical nature of Hopf-bifurcating periodic solution is determined by positive and negative signs of the real part of Φ , where

$$\Phi = -a_l F_{u_j u_m u_s}^l b_j b_m \bar{b}_s + 2a_l F_{u_j u_m}^l b_j (J_{E^*}^{-1})_{mr} F_{u_p u_q}^r b_p \bar{b}_q + a_l F_{u_j u_k}^l \bar{b}_j [(J_{E^*} - 2i\omega_0)^{-1}]_{kr} F_{u_p u_q}^r b_p b_q$$

where the repeated indices within each term imply a sum from 1 to 3 and all the derivatives of F^l are evaluated at the equilibrium E^* with $u_1 = x$, $u_2 = y_J$, $u_3 = y_A$ and J_{E^*} is the variational matrix of (2) calculated at E^* . $[(J_{E^*})^{-1}]_{mr}$ denotes the element in row m , column r of $(J_{E^*})^{-1}$. Also, $\mathbf{a} = (a_1, a_2, a_3)$ and $\mathbf{b} = (b_1, b_2, b_3)^T$ are left and right normalized eigenvectors of J_{E^*} with respect to the eigenvalues $\pm i\omega_0$ at $r = r_{cr}$ so that $\mathbf{a} \cdot \mathbf{b} = 1$.

Now, at E^* , all the second- and third-order derivatives of F^l ($l = 1, 2, 3$) are as follows:

$$\begin{aligned} F_{xx}^1 &= -\frac{2r}{K} + \frac{2m_1 a_1 y_A^*}{(a_1 + x^*)^3}, F_{xy_A}^1 = F_{y_A x}^1 = -\frac{m_1 a_1}{(a_1 + x^*)^2}, F_{xxx}^1 = -\frac{6m_1 a_1 y_A^*}{(a_1 + x^*)^4}, \\ F_{x y_J}^1 &= F_{y_J x}^1 = F_{y_A x}^1 = \frac{2m_1 a_1}{(a_1 + x^*)^3}, F_{xx}^2 = -\frac{2e_1 m_1 a_1 y_A^*}{(a_1 + x^*)^3}, F_{y_J y_J}^2 = \frac{2(1 - e_2)m_2 a_2 y_A^*}{(a_2 + y_J^*)^3}, \\ F_{y_J y_A}^2 &= F_{y_A y_J}^2 = -\frac{(1 - e_2)m_2 a_2}{(a_2 + y_J^*)^2}, F_{x y_A}^2 = F_{y_A x}^2 = \frac{e_1 m_1 a_1}{(a_1 + x^*)^2}, F_{xxx}^2 = \frac{6e_1 m_1 a_1 y_A^*}{(a_1 + x^*)^4}, \\ F_{y_J y_J}^2 &= -\frac{6(1 - e_2)m_2 a_2 y_A^*}{(a_2 + y_J^*)^4}, F_{x y_J}^2 = F_{y_J x}^2 = F_{y_A x}^2 = -\frac{2e_1 m_1 a_1}{(a_1 + x^*)^3}, \\ F_{y_J y_A}^2 &= F_{y_A y_J}^2 = F_{y_A y_J}^2 = \frac{2(1 - e_2)m_2 a_2}{(a_2 + y_J^*)^3}, F_{y_A y_A}^3 = \frac{2hc}{(c + y_A^*)^3}, \\ F_{y_A y_A y_A}^3 &= -\frac{6hc}{(c + y_A^*)^4}. \end{aligned}$$

Also, at E^* we obtain $(J_{E^*} - 2i\omega_0)^{-1} = (Q_{\omega_0}^{ij})_{3 \times 3}$ where

$$\begin{aligned} Q_{\omega_0}^{11} \Delta &= (F_{y_J y_A}^2 F_{y_A}^3 - \mu F_{y_A}^2 - 4\omega_0^2) - 2i\omega_0 (F_{y_J}^2 + F_{y_A}^3), Q_{\omega_0}^{12} \Delta = \mu F_{y_A}^1, \\ Q_{\omega_0}^{13} \Delta &= -F_{y_A}^1 (F_{y_J}^2 - 2i\omega_0), Q_{\omega_0}^{21} \Delta = -F_x^2 (F_{y_A}^3 - 2i\omega_0), \\ Q_{\omega_0}^{22} \Delta &= (F_x^1 F_{y_A}^3 - 4\omega_0^2) - 2i\omega_0 (F_x^1 + F_{y_A}^3), \\ Q_{\omega_0}^{23} \Delta &= (F_x^2 F_{y_A}^1 - F_x^1 F_{y_A}^2) + 2i\omega_0 F_{y_A}^2, \\ Q_{\omega_0}^{31} \Delta &= \mu F_x^2, Q_{\omega_0}^{32} \Delta = -\mu (F_x^1 - 2i\omega_0), \\ Q_{\omega_0}^{33} \Delta &= (F_x^1 F_{y_J}^2 - 4\omega_0^2) - 2i\omega_0 (F_x^1 + F_{y_J}^2) \text{ and} \\ \Delta &= F_x^1 (F_{y_J}^2 F_{y_A}^3 - \mu F_{y_A}^2 - 4\omega_0^2) + \mu F_{y_A}^1 F_x^2 - 4\omega_0 (F_{y_J}^2 + F_{y_A}^3) \\ &\quad - 2i\omega_0 \{ F_{y_J}^2 F_{y_A}^3 - \mu F_{y_A}^2 - 4\omega_0^2 + F_x^1 (F_{y_J}^2 + F_{y_A}^3) \}. \end{aligned}$$

Putting $\omega_0 = 0$ in the above expressions, we get the components of $(J_{E^*})^{-1} = (Q^{ij})_{3 \times 3}$.

The left and right normalized eigenvectors $\mathbf{a} = (a_1, a_2, a_3)$ and $\mathbf{b} = (b_1, b_2, b_3)^T$ of variational matrix J_{E^*} are

$$\mathbf{a} = \frac{\xi_1}{\mu F_x^2} \left(\mu F_x^2, \mu (i\omega_0 - F_x^1), (F_x^1 F_{y_j}^2 - \omega_0^2) - i\omega_0 (F_x^1 + F_{y_j}^2) \right) \text{ and}$$

$$\mathbf{b} = \frac{\xi_2}{\mu F_{y_A}^1} \left(\mu F_{y_A}^1, (F_x^1 F_{y_A}^3 - \omega_0^2) - i\omega_0 (F_x^1 + F_{y_A}^3), \mu (i\omega_0 - F_x^1) \right)^T \text{ where } \xi_1, \xi_2 \text{ are}$$

complex numbers. Using $\mathbf{a} \cdot \mathbf{b} = 1$ we obtain $\xi_1 \xi_2 = \frac{\mu^2 F_{y_A}^1 F_x^2 (\psi_1 + i\omega_0 \psi_2)}{\psi_1^2 + \omega_0^2 \psi_2^2}$

where $\psi_1 = F_{y_A}^1 F_x^2 - \omega_0^2 \mu + \mu (F_x^1)^2 + ((F_x^1)^2 - \omega_0^2) (F_{y_j}^2 F_{y_A}^3 - \omega_0^2) - 2\omega_0^2 F_x^1 \times (F_{y_j}^2 + F_{y_A}^3)$ and $\psi_2 = 2\mu F_x^1 + 2F_x^1 (F_{y_j}^2 F_{y_A}^3 - \omega_0^2) + (F_{y_j}^2 + F_{y_A}^3) ((F_x^1)^2 - \omega_0^2)$.

$$\begin{aligned} \text{Now } -a_l F_{u_j u_m u_s}^l b_j b_m \bar{b}_s &= -(a_1 F_{xxx}^1 + a_2 F_{xxx}^2) b_1 |b_1|^2 - a_2 F_{y_j y_j y_A}^2 b_2 |b_2|^2 - \\ &a_3 F_{y_A y_A y_A}^3 b_3 |b_3|^2 - (a_1 F_{xxy_A}^1 + a_2 F_{xxy_A}^2) (2b_3 |b_1|^2 + b_1^2 \bar{b}_3) - a_2 F_{y_j y_j y_A}^2 (b_2^2 \bar{b}_3 + 2b_3 \bar{b}_2^2), \\ 2a_l F_{u_j u_m}^l b_j (J_{E^*}^{-1})_{mr} F_{u_\mu u_q}^r b_p \bar{b}_q &= 2 \left[a_1 (F_{xx}^1 b_1 + F_{y_A x}^1 b_3) + a_2 (F_{xx}^2 b_1 + F_{y_A x}^2 b_3) \right] (Q^{11} A_1 + \\ &Q^{12} A_2 + Q^{13} A_3) + 2a_2 (F_{y_A y_j}^2 b_3 + F_{y_j y_j}^2 b_2) (Q^{21} A_1 + Q^{22} A_2 + Q^{23} A_3) + 2[a_1 F_{xy_A}^1 b_1 + \\ &a_2 (F_{xy_A}^2 b_1 + F_{y_j y_A}^2 b_2) + a_3 F_{y_A y_A}^3 b_3] (Q^{31} A_1 + Q^{32} A_2 + Q^{33} A_3) \text{ and } a_l F_{u_j u_k}^l \bar{b}_j \\ &[(J_{E^*} - 2i\omega_0)^{-1}]_{kr} F_{u_\mu u_q}^r b_p \bar{b}_q = [a_1 (F_{xx}^1 \bar{b}_1 + F_{y_A x}^1 \bar{b}_3) + a_2 (F_{xx}^2 \bar{b}_1 + F_{y_A x}^2 \bar{b}_3)] (Q_{\omega_0}^{11} A^1 + \\ &Q_{\omega_0}^{12} A^2 + Q_{\omega_0}^{13} A^3) + a_2 (F_{y_j y_j}^2 \bar{b}_2 + F_{y_A y_j}^2 \bar{b}_3) (Q_{\omega_0}^{21} A^1 + Q_{\omega_0}^{22} A^2 + Q_{\omega_0}^{23} A^3) + \{a_1 F_{xy_A}^1 \bar{b}_1 + \\ &a_2 (F_{xy_A}^2 \bar{b}_1 + F_{y_j y_A}^2 \bar{b}_2) + a_3 F_{y_A y_A}^3 \bar{b}_3\} (Q_{\omega_0}^{31} A^1 + Q_{\omega_0}^{32} A^2 + Q_{\omega_0}^{33} A^3) \text{ where } A_1 = F_{xx}^1 |b_1|^2 + \\ &F_{xy_A}^1 (b_1 \bar{b}_3 + b_3 \bar{b}_1), A_2 = F_{xx}^2 |b_1|^2 + F_{xy_A}^2 (b_1 \bar{b}_3 + b_3 \bar{b}_1) + F_{y_j y_A}^2 (b_2 \bar{b}_3 + b_3 \bar{b}_2) + F_{y_j y_j}^2 \bar{b}_2^2, \\ &A_3 = F_{y_A y_A}^3 |b_3|^2, A^1 = F_{xx}^1 b_1^2 + 2F_{xy_A}^1 b_1 b_3, A^2 = F_{xx}^2 b_1^2 + F_{y_j y_j}^2 b_2^2 + 2F_{y_A x}^2 b_1 b_3 + \\ &2F_{y_j y_A}^2 b_2 b_3, A^3 = F_{y_A y_A}^3 b_3^2. \end{aligned}$$

For these values of $F_{u_j u_k}^l, F_{u_i u_j}^l, \mathbf{a}, \mathbf{b}$ and components Q^{ij} and $Q_{\omega_0}^{ij}$, we obtain the value of $(\Phi)_{h=h_{cr}}$. If $(\Phi)_{h=h_{cr}} > 0$, then the system (3) undergoes a supercritical Hopf bifurcation as h is increased through h_{cr} so that the bifurcating periodic orbit is asymptotically orbitally stable.

Thus we observe that in the absence of the delay, *Pterois volitans* will not survive in the system if the maximal harvesting rate exceeds a certain threshold. Also, with high levels of predation by adult *Pterois volitans* on *Parrotfish*, the system exhibits dynamic instability. In this situation, a subcritical Hopf bifurcation occurs as the maximal harvesting rate is increased through a critical value.

5 Qualitative analysis of the model at the boundary with maturation time delay ($\tau \neq 0$)

We note that the characteristic equation for the variational matrix about the steady state E_0 with time delay remains the same as that obtained for the non-delayed system about E_0 .

The characteristic equation of the system (1) at E_1 is

$$D_{E_1}(\lambda, \tau) = \lambda^3 + A_1 \lambda^2 + B_1 \lambda + C_1 - e^{-\lambda \tau} (A_2 \lambda + B_2) = 0 \quad (3)$$

where $A_1 = r + \mu + D_1 + D_2 + \frac{h}{c}$, $B_1 = r(\mu + D_1 + D_2 + \frac{h}{c}) + (\mu + D_1)(D_2 + \frac{h}{c})$, $C_1 = r(\mu + D_1)(D_2 + \frac{h}{c})$, $A_2 = \frac{e_1 m_1 K \mu}{a_1 + K}$ and $B_2 = rA_2$.

Lemma 5.1 *A sufficient condition for E_1 to be locally asymptotically stable is $Q_1 > 0$, $Q_3 > \frac{Q_2^2}{4Q_1}$ and $h > c \left\{ \frac{e_1 m_1 K \mu}{(a_1 + K)(\mu + D_1)} - D_2 \right\}$, where $Q_1 = A_1^2 - 2B_1$, $Q_2 = B_1^2 - 2A_1C_1 - A_2^2$, $Q_3 = C_1^2 - B_2^2$.*

Proof The system (1) is locally asymptotically stable at E_1 for all $\tau \geq 0$ if the following conditions given by Gopalsamy [29] and Beretta and Kuang [30] hold:

- (a) the real parts of all the roots of $D_{E_1}(\lambda, 0) = 0$ are negative,
- (b) for all real ω and any $\tau \geq 0$, $D_{E_1}(i\omega, \tau) \neq 0$ where $i = \sqrt{-1}$.

We have $D_{E_1}(i\omega, \tau) = (-A_1\omega^2 + C_1 - B_2\cos\omega\tau - A_2\omega\sin\omega\tau) + i(-\omega^3 + B_1\omega - \omega A_2\cos\omega\tau + B_2\sin\omega\tau)$.

$D_{E_1}(i\omega, \tau) = 0$ implies $-A_1\omega^2 + C_1 = B_2\cos\omega\tau + A_2\omega\sin\omega\tau$ and $-\omega^3 + B_1\omega = \omega A_2\cos\omega\tau - B_2\sin\omega\tau$.

Now, $(-A_1\omega^2 + C_1)^2 + (-\omega^3 + B_1\omega)^2 = \omega^2 A_2^2 + B_1^2$ gives $\omega^6 + Q_1\omega^4 + Q_2\omega^2 + Q_3 = 0$, where $Q_1 = A_1^2 - 2B_1$, $Q_2 = B_1^2 - 2A_1C_1 - A_2^2$ and $Q_3 = C_1^2 - B_2^2$.

Sufficient conditions for the nonexistence of a real number ω satisfying $D_{E_1}(i\omega, \tau) = 0$ can be written as:

$$\omega^6 + Q_1\omega^4 + Q_2\omega^2 + Q_3 > 0 \Rightarrow \omega^6 + Q_1\left(\omega^2 + \frac{Q_2}{2Q_1}\right)^2 + Q_3 - \frac{Q_2^2}{4Q_1} > 0.$$

Thus, for all real ω and for any $\tau \geq 0$, $D_{E_1}(i\omega, \tau) \neq 0$ if $Q_1 > 0$ and $Q_3 > \frac{Q_2^2}{4Q_1}$.

Also, the real parts of all the roots of $D_{E_1}(\lambda, 0) = 0$ are negative if $h > c \left\{ \frac{e_1 m_1 K \mu}{(a_1 + K)(\mu + D_1)} - D_2 \right\}$.

Therefore, the statement of Lemma 5.1 holds. $\square$

5.1 Estimation of the length of delay to preserve stability at E_1

It is well known that time delays in ecological systems may introduce instability into the system [31]. Therefore, we shall first derive estimates for the length of the delay for which an equilibrium which is stable with no delay continues to remain stable. For this, we assume that in the absence of delays, E_1 is locally asymptotically stable.

Lemma 5.1.1 *If $h > c \left\{ \frac{e_1 m_1 K \mu}{(a_1 + K)(\mu + D_1)} - D_2 \right\}$ holds and if there exists a τ in $0 \leq \tau \leq \tau_+$ such that $A_\theta \tau^2 + B_\theta \tau > C_\theta$, then τ_+ is the maximum value (length of delay) for which E_1 is asymptotically stable, where $A_\theta = \frac{1}{2}|A_2|v_+^2$, $B_\theta = |B_2|$ and $C_\theta = v_+^2 - B_1$.*

Proof Let $u(t)$, $v_J(t)$ and $v_A(t)$ be the respective linearized variables of this model. Then system (1) becomes

$$\begin{aligned}\frac{du}{dt} &= -ru(t) - \frac{m_1 K}{a_1 + K} v_A(t) \\ \frac{dv_J}{dt} &= -(\mu + D_1) v_J(t) + \frac{e_1 m_1 K}{a_1 + K} v_A(t - \tau) \\ \frac{dv_A}{dt} &= \mu v_J(t) - \left(D_2 + \frac{h}{c}\right) v_A(t)\end{aligned}\quad (4)$$

Let $\bar{u}(s)$, $\bar{v}_J(s)$ and $\bar{v}_A(s)$ be the Laplace transforms of $u(t)$, $v_J(t)$ and $v_A(t)$, respectively. Taking the Laplace transformation of system (4), we have

$$\begin{aligned}(s + r) \bar{u}(s) &= \frac{-m_1 K}{a_1 + K} \bar{v}_A(s) + u(0) \\ (s + \mu + D_1) \bar{v}_J(s) &= \left(\frac{e_1 m_1 K e^{-s\tau}}{a_1 + K}\right) (\bar{v}_A(s) + C_1(s)) + v_J(0) \\ \left(s + D_2 + \frac{h}{c}\right) \bar{v}_A(s) &= \mu \bar{v}_J(s) + v_A(0)\end{aligned}$$

where $C_1(s) = \int_{-\tau}^0 e^{-st} v_A(t) dt$.

The inverse Laplace transform of $\bar{u}(s)$, $\bar{v}_J(s)$ and $\bar{v}_A(s)$ will have terms which exponentially increase with time, if $\bar{u}(s)$, $\bar{v}_J(s)$ and $\bar{v}_A(s)$ have a pole with positive real parts. Since E_1 needs to be locally asymptotically stable, it is necessary and sufficient that all poles of $\bar{u}(s)$, $\bar{v}_J(s)$ and $\bar{v}_A(s)$ have negative real parts. We shall employ the Nyquist criterion, which states that if s is the arc length of a curve encircling the right half-plane, the curve $\bar{u}(s)$, $\bar{v}_J(s)$ and $\bar{v}_A(s)$ will encircle the origin a number of times equal to the difference between the number of poles and the number of zeroes of $\bar{u}(s)$, $\bar{v}_J(s)$ and $\bar{v}_A(s)$ in the right half-plane [32]. Let $F(s) = s^3 + A_1 s^2 + B_1 s + C_1 - e^{-s\tau} (A_2 s + B_2)$ (from (3)).

Then E_1 is locally asymptotically stable if $\operatorname{Re}\{F(iv_0)\} = 0$ and $\operatorname{Im}\{F(iv_0)\} > 0$, where v_0 is the smallest positive root of $\operatorname{Re}\{F(iv_0)\} = 0$ [31].

Now, $\operatorname{Re}\{F(iv_0)\} = 0 \Rightarrow -A_1 v_0^2 + C_1 = B_2 \cos v_0 \tau + A_2 v_0 \sin v_0 \tau$ and $\operatorname{Im}\{F(iv_0)\} > 0 \Rightarrow -v_0^3 + B_1 v_0 > v_0 A_2 \cos v_0 \tau - B_2 \sin v_0 \tau$.

Therefore, E_1 will be stable if the inequality $-v^3 + B_1 v > v A_2 \cos v \tau - B_2 \sin v \tau$ holds at $v = v_0$, where v_0 is the first positive root of $-A_1 v^2 + C_1 = B_2 \cos v \tau + A_2 v \sin v \tau$.

We shall now estimate an upper bound v_+ of v_0 , which would be independent of τ . Then we estimate τ so that $-v^3 + B_1 v > v A_2 \cos v \tau - B_2 \sin v \tau$ holds for all values of v , $0 \leq v \leq v_+$, and hence in particular at $v = v_0$.

Maximizing $-A_1 v^2 + C_1 = B_2 \cos v \tau + A_2 v \sin v \tau$ subject to the restriction that $|\sin v \tau| \leq 1$ and $|\cos v \tau| \leq 1$ we obtain $A_1 v^2 + |A_2| v - (C_1 - B_2) = 0$.

Now, the greatest positive root of $A_1 v^2 + |A_2| v - (C_1 - B_2) = 0$ is given by $v_+ = \frac{-|A_2| + \sqrt{A_2^2 + 4A_1(C_1 - B_2)}}{2A_1} \geq v_0$.

Thus, we can find an upper bound of v , namely, v_+ (with $v_0 \leq v_+$) for which the inequality $-v^3 + B_1 v > v A_2 \cos v \tau - B_2 \sin v \tau$ holds. Also, v_+ is independent of the delay τ .

Again, using $|\sin v \tau| \leq v \tau$ and $|1 - \cos v \tau| = 2 \sin^2 \frac{v \tau}{2} \leq \frac{1}{2} v^2 \tau^2$ we obtain $A_\theta \tau^2 + B_\theta \tau > C_\theta$, where $A_\theta = \frac{1}{2} |A_2| v_+^2$, $B_\theta = |B_2|$ and $C_\theta = v_+^2 - B_1$.

Then, Nyquist criterion holds for $0 \leq \tau \leq \tau_+$, where $\tau_+ = \frac{-B_\theta + \sqrt{B_\theta^2 + 4A_\theta C_\theta}}{2A_\theta}$ is an estimate for the length of delay for which the stability of the system at E_1 is preserved [32]. $\square$

6 Qualitative analysis of the model at E^* with maturation time delay ($\tau \neq 0$)

The characteristic equation of the system at E^* is $\bar{D}(\lambda, \tau) = \lambda^3 + A_{11}\lambda^2 + B_{11}\lambda + C_{11} + e^{-\lambda\tau}(A_{12}\lambda^2 + B_{12}\lambda + C_{12}) = 0$ where

$$\begin{aligned} A_{11} &= \mu + D_1 + D_2 + \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} + \frac{(1 - e_2)m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} + \frac{hc}{(c + y_A^*)^2} - r \left(1 - \frac{2x^*}{K}\right), \\ A_{12} &= -\frac{e_2 m_2 a_2 y_A^*}{(a_2 + y_J^*)^2}, \\ B_{11} &= \left\{ D_2 + \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} + \frac{hc}{(c + y_A^*)^2} - r \left(1 - \frac{2x^*}{K}\right) \right\} \left\{ \mu + D_1 + \frac{(1 - e_2)m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} \\ &\quad - \left\{ r \left(1 - \frac{2x^*}{K}\right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} \right\} \left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} + \frac{m_2 \mu y_J^*}{a_2 + y_J^*}, \\ B_{12} &= \frac{e_2 m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \left\{ r \left(1 - \frac{2x^*}{K}\right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} - D_2 - \frac{hc}{(c + y_A^*)^2} \right\} \\ &\quad - \mu \left(\frac{e_1 m_1 x^*}{a_1 + x^*} + \frac{e_2 m_2 y_J^*}{a_2 + y_J^*} \right), \\ C_{11} &= -\mu \left\{ r \left(1 - \frac{2x^*}{K}\right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} \right\} \frac{m_2 y_J^*}{a_2 + y_J^*} \\ &\quad - \left\{ r \left(1 - \frac{2x^*}{K}\right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} \right\} \left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \left\{ \mu + D_1 + \frac{m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} \\ C_{12} &= \mu \left\{ r \left(1 - \frac{2x^*}{K}\right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} \right\} \left(\frac{e_1 m_1 x^*}{a_1 + x^*} + \frac{e_2 m_2 y_J^*}{a_2 + y_J^*} \right) \\ &\quad + \left\{ r \left(1 - \frac{2x^*}{K}\right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2} \right\} \left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \frac{e_2 m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} + \frac{m_1^2 a_1 x^* y_A^*}{(a_1 + x^*)^2}. \end{aligned}$$

Lemma 6.1.1 *A sufficient condition for E^* to be locally asymptotically stable is $h > \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1)m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\}$, $\eta > 0$, $\bar{Q}_1 > 0$ and $\bar{Q}_3 > \frac{\bar{Q}_2^2}{4\bar{Q}_1}$.*

Proof From Lemma 4.6, it follows that the real parts of all the roots of $\bar{D}(\lambda, 0) = 0$ are negative if

$$h > \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1)m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\} \text{ and } \eta > 0.$$

Now, $\bar{D}(i\omega, t) = 0$ gives

$$\begin{aligned} -A_{11}\omega^2 + C_{11} &= A_{12}\omega^2 \cos\omega\tau - C_{12}\cos\omega\tau - B_{12}\omega \sin\omega\tau \text{ and} \\ -\omega^3 + B_{11}\omega &= -B_{12}\omega \cos\omega\tau - A_{12}\omega^2 \sin\omega\tau + C_{12}\sin\omega\tau \end{aligned}$$

This gives $\omega^6 + \bar{Q}_1\omega^4 + \bar{Q}_2\omega^2 + \bar{Q}_3 = 0$, where $\bar{Q}_1 = A_{11}^2 - 2B_{11} - A_{12}^2$, $\bar{Q}_2 = B_{11}^2 - 2A_{11}C_{11} + 2A_{12}C_{12} - B_{12}^2$ and $\bar{Q}_3 = C_{11}^2 - C_{12}^2$.

Sufficient conditions for the nonexistence of a real number ω satisfying $\bar{D}(i\omega, \tau) = 0$ can be written as:

$$\omega^6 + \bar{Q}_1 \omega^4 + \bar{Q}_2 \omega^2 + \bar{Q}_3 > 0 \Rightarrow \omega^6 + \bar{Q}_1 \left(\omega^2 + \frac{\bar{Q}_2}{2\bar{Q}_1} \right)^2 + \bar{Q}_3 - \frac{\bar{Q}_2^2}{4\bar{Q}_1} > 0.$$

Thus, for all real ω and for any $\tau \geq 0$, $\bar{D}(i\omega, \tau) \neq 0$ if $\bar{Q}_1 > 0$ and $\bar{Q}_3 > \frac{\bar{Q}_2^2}{4\bar{Q}_1}$.

Therefore, the statement of Lemma 6.1.1 is proved.

6.1 Estimation of the length of delay to preserve stability at E^*

Lemma 6.2 *If the system (2) is stable at E^* and if there exists a τ in $0 \leq \tau \leq \bar{\tau}_+$ such that $\bar{A}_\theta \tau^2 + \bar{B}_\theta \tau + \bar{C}_\theta > 0$ holds, then $\bar{\tau}_+$ is the maximum value (length of delay) for which the system (1) is locally asymptotically stable at E^* , where $\bar{A}_\theta = \frac{1}{2} \bar{v}_+^2 |B_{12}|$, $\bar{B}_\theta = |C_{12}|$ and $\bar{C}_\theta = \bar{v}_+ |A_{12}| + B_{11} - \bar{v}_+^2$.*

Proof Then system (1) can be expressed as

$$\begin{aligned} \frac{du}{dt} &= a_{11}u(t) + a_{12}v_A(t) \\ \frac{dv_J}{dt} &= a_{21}v_J(t) + a_{22}v_A(t) + a_{23}u(t - \tau) + a_{24}v_J(t - \tau) + a_{25}v_A(t - \tau) \\ \frac{dv_A}{dt} &= a_{31}v_J(t) + a_{32}v_A(t) \end{aligned} \quad (5)$$

where

$$\begin{aligned} a_{11} &= r \left(1 - \frac{2x^*}{K} \right) - \frac{m_1 a_1 y_A^*}{(a_1 + x^*)^2}, \quad a_{12} = -\frac{m_1 x^*}{a_1 + x^*}, \quad a_{21} = -\mu - D_1 - \frac{m_2 a_2 y_A^*}{(a_2 + y_J^*)^2}, \\ a_{22} &= -\frac{m_2 y_J^*}{a_1 + y_J^*}, \quad a_{23} = \frac{e_1 m_1 a_1 y_A^*}{(a_1 + x^*)^2}, \quad a_{24} = \frac{e_2 m_2 a_2 y_A^*}{(a_2 + y_J^*)^2}, \quad a_{25} = \frac{e_1 m_1 x^*}{a_1 + x^*} + \frac{e_2 m_2 y_J^*}{a_2 + y_J^*}, \\ a_{31} &= \mu, \quad a_{32} = -D_2 - \frac{hc}{(c + y_A^*)^2} \end{aligned}$$

Taking the Laplace transformation of system (5), we have

$$\begin{aligned} (s - a_{11}) \bar{u}(s) &= b_{12} \bar{v}_A(s) + u(0) \\ (s - a_{21}) \bar{v}_J(s) &= a_{22} \bar{v}_A(s) + a_{23} e^{-s\tau} (\bar{u}(s) + K_1(s)) + a_{24} e^{-s\tau} \\ &\quad \times (\bar{v}_J(s) + K_2(s)) (t - \tau) + a_{25} e^{-s\tau} (\bar{v}_A(s) + K_3(s)) + v_J(0) \\ (s - b_{32}) &= b_{31} \bar{v}_J(s) + v_A(0) \end{aligned}$$

where $K_1(s) = \int_{-\tau}^0 e^{-st} u(t) dt$, $K_2(s) = \int_{-\tau}^0 e^{-st} v_J(t) dt$ and $K_3(s) = \int_{-\tau}^0 e^{-st} v_A(t) dt$. Let $\bar{F}(s) = s^3 + A_{11}s^2 + B_{11}s + C_{11} + e^{-s\tau} (A_{12}s^2 + B_{12}s + C_{12}) = 0$. Also, let $\bar{v}_0$ be the smallest positive root of $\text{Re} \{ \bar{F}(iv) \} = 0$.

Then E^* is locally asymptotically stable if $-A_{11} \bar{v}_0^2 + C_{11} = A_{12} \bar{v}_0^2 \cos \bar{v}_0 \tau - C_{12} \cos \bar{v}_0 \tau - B_{12} \bar{v}_0 \sin \bar{v}_0 \tau$ and $-\bar{v}_0^3 + B_{11} \bar{v}_0 > -B_{12} \bar{v}_0 \cos \bar{v}_0 \tau - A_{12} \bar{v}_0^2 \sin \bar{v}_0 \tau + C_{12} \sin \bar{v}_0 \tau$.

Now, $-A_{11} v^2 + C_{11} \leq |A_{12}| v^2 + v |B_{12}| + |C_{12}|$.

Therefore, the positive solution $\bar{v}_+$ of $(A_{11} + |A_{12}|)v^2 + v|B_{12}| - (C_{11} - |C_{12}|) = 0$ is always greater than or equal to $\bar{v}_0$.

We obtain

$$\bar{v}_+ = \frac{-|B_{12}| + \sqrt{B_{12}^2 + 4(A_{11} + |A_{12}|)(C_{11} - |C_{12}|)}}{2(A_{11} + |A_{12}|)} \geq \bar{v}_0,$$

where $\bar{v}_+$ is independent of τ .

Also,

$$-v^3 + B_{11}v > -B_{12}v \cos v\tau - A_{12}v^2 \sin v\tau + C_{12} \sin v\tau \Rightarrow -v^2 + B_{11} > -|B_{12}|(1 + \frac{1}{2}\tau^2 v^2) - |C_{12}|\tau - |A_{12}|v \Rightarrow \bar{A}_\theta \tau^2 + \bar{B}_\theta \tau + \bar{C}_\theta > 0 \text{ where } \bar{A}_\theta = \frac{1}{2}\bar{v}_+^2 |B_{12}|, \bar{B}_\theta = |C_{12}| \text{ and } \bar{C}_\theta = \bar{v}_+ |A_{12}| + B_{11} - \bar{v}_+^2.$$

Therefore, $\bar{\tau}_+ = \frac{-\bar{B}_\theta + \sqrt{\bar{B}_\theta^2 - 4\bar{A}_\theta \bar{C}_\theta}}{2\bar{A}_\theta}$ is an estimate for the length of delay for which the stability of the system at E^* is preserved.

7 Bifurcation analysis in the presence of discrete delay

We consider the system with a discrete time delay governed by the system (1). The stability of the equilibrium point can be determined by the sign of the real part of the eigenvalues determined by the characteristic equation $\bar{D}(\lambda, u) = 0$.

Lemma 7.1 *If $\bar{Q}_1 > 0$ and $\bar{Q}_3 > \frac{\bar{Q}_2^2}{4\bar{Q}_1}$, then a Hopf bifurcation occurs as τ crosses $\hat{\tau}$, where*

$$\hat{\tau} = \frac{1}{\hat{\beta}} \arctan \left[\frac{\hat{\beta} \left\{ \hat{\beta}^4 A_{12} + \hat{\beta}^2 (A_{11} B_{12} - A_{12} B_{11} - C_{12}) + B_{11} C_{12} - B_{12} C_{11} \right\}}{\hat{\beta}^4 (B_{12} - A_{11} A_{12}) + \hat{\beta}^2 (A_{11} C_{12} + A_{12} C_{11} - B_{11} B_{12}) - C_{11} C_{12}} \right].$$

Proof Let $\lambda = \alpha + i\beta$. Then, separating the real and imaginary parts of $\bar{D}(\lambda, \tau) = 0$, we obtain the following system of transcendental equations:

$$\begin{aligned} \alpha^3 - 3\alpha\beta^2 + A_{11}(\alpha^2 - \beta^2) + B_{11}\alpha + C_{11} &= -e^{-\alpha\tau} \{A_{12}(\alpha^2 - \beta^2) + B_{12}\alpha + C_{12}\} \\ &\times \cos\beta\tau - e^{-\alpha\tau} (2\alpha\beta A_{12} + \beta B_{12}) \sin\beta\tau \end{aligned} \quad (6)$$

$$\begin{aligned} -\beta^3 + 3\alpha^2\beta + 2\alpha\beta A_{11} + \beta B_{11} &= -e^{-\alpha\tau} (2\alpha\beta A_{12} + \beta B_{12}) \cos\beta\tau \\ + e^{-\alpha\tau} \{A_{12}(\alpha^2 - \beta^2) + B_{12}\alpha + C_{12}\} &\sin\beta\tau \end{aligned} \quad (7)$$

We are interested to know the change of stability at E^* which will occur at $\tau = \hat{\tau}$ for which $\alpha = 0$ and $\beta \neq 0$. Then $\alpha(\hat{\tau}) = 0$ and $\beta(\hat{\tau}) = \hat{\beta} \neq 0$ gives

$$-\hat{\beta}^2 A_{11} + C_{11} = (A_{12} \hat{\beta}^2 - C_{12}) \cos(\hat{\beta} \hat{\tau}) - B_{12} \hat{\beta} \sin(\hat{\beta} \hat{\tau}) \quad (8)$$

$$-\hat{\beta}^3 + \hat{\beta} B_{11} = -\hat{\beta} B_{12} \cos(\hat{\beta} \hat{\tau}) + (C_{12} - A_{12} \hat{\beta}^2) \sin(\hat{\beta} \hat{\tau}) \quad (9)$$

Squaring both sides of (8) and (9) and then adding we get $\hat{\beta}^6 + (A_{11}^2 - 2B_{11} - A_{12}^2)\hat{\beta}^4 + (B_{11} - 2A_{11}C_{11} + 2A_{12}C_{12} - B_{12}^2)\hat{\beta}^2 + (C_{11}^2 - C_{12}^2) = 0$.

Also, from (6) and (7) we get

$$\sin(\hat{\beta}\hat{\tau}) = \frac{\hat{\beta}(A_{12}\hat{\beta}^2 - C_{12})(\hat{\beta}^2 - B_{11}) + \hat{\beta}B_{12}(\hat{\beta}^2 A_{11} - C_{11})}{B_{12}^2\hat{\beta}^2 + (A_{12}\hat{\beta}^2 - C_{12})^2}$$

$$\cos(\hat{\beta}\hat{\tau}) = \frac{B_{12}\hat{\beta}^2(\hat{\beta}^2 - B_{11}) - (\hat{\beta}^2 A_{11} - C_{11})(A_{12}\hat{\beta}^2 - C_{12})}{B_{12}^2\hat{\beta}^2 + (A_{12}\hat{\beta}^2 - C_{12})^2}$$

Thus, $\hat{\tau}_n = \frac{1}{\hat{\beta}} \arctan \left[\frac{\hat{\beta} \{ \hat{\beta}^4 A_{12} + \hat{\beta}^2 (A_{11} B_{12} - A_{12} B_{11} - C_{12}) + B_{11} C_{12} - B_{12} C_{11} \}}{\hat{\beta}^4 (B_{12} - A_{11} A_{12}) + \hat{\beta}^2 (A_{11} C_{12} + A_{12} C_{11} - B_{11} B_{12}) - C_{11} C_{12}} \right] + \frac{n\pi}{\hat{\beta}}, n = 0, 1, 2, \dots$

The smallest $\hat{\tau}_n$ is given by $n = 0$ and we take it as

$$\hat{\tau} = \frac{1}{\hat{\beta}} \arctan \left[\frac{\hat{\beta} \{ \hat{\beta}^4 A_{12} + \hat{\beta}^2 (A_{11} B_{12} - A_{12} B_{11} - C_{12}) + B_{11} C_{12} - B_{12} C_{11} \}}{\hat{\beta}^4 (B_{12} - A_{11} A_{12}) + \hat{\beta}^2 (A_{11} C_{12} + A_{12} C_{11} - B_{11} B_{12}) - C_{11} C_{12}} \right]$$

Differentiating (6) and (7) with respect to τ at $\tau = \hat{\tau}$ we obtain

$$L \frac{d\alpha}{d\tau}(\hat{\tau}) + M \frac{d\beta}{d\tau}(\hat{\tau}) = X$$

$$-M \frac{d\alpha}{d\tau}(\hat{\tau}) + L \frac{d\beta}{d\tau}(\hat{\tau}) = Y$$

where

$$L = -3\hat{\beta}^2 + B_{11} - \hat{\tau}(C_{12} - \hat{\beta}^2 A_{12}) \cos \hat{\beta}\hat{\tau} + B_{12} \cos \hat{\beta}\hat{\tau} - \hat{\tau} \hat{\beta} B_{12} \sin \hat{\beta}\hat{\tau} + 2\hat{\beta} A_{12} \sin \hat{\beta}\hat{\tau}$$

$$M = -2\hat{\beta} A_{11} - \hat{\tau}(C_{12} - \hat{\beta}^2 A_{12}) \sin \hat{\beta}\hat{\tau} - 2\hat{\beta} A_{12} \cos \hat{\beta}\hat{\tau} + \hat{\tau} \hat{\beta} B_{12} \cos \hat{\beta}\hat{\tau} + B_{12} \sin \hat{\beta}\hat{\tau}$$

$$X = \hat{\beta}(C_{12} - \hat{\beta}^2 A_{12}) \sin \hat{\beta}\hat{\tau} - \hat{\tau}^2 B_{12} \cos \hat{\beta}\hat{\tau}$$

$$Y = \hat{\beta}^2 B_{12} \sin \hat{\beta}\hat{\tau} + \hat{\beta}(C_{12} - \hat{\beta}^2 A_{12}) \cos \hat{\beta}\hat{\tau}$$

Solving for $\frac{d\alpha}{d\tau}$ at $\tau = \hat{\tau}$ we get $\frac{d\alpha}{d\tau}(\hat{\tau}) = \frac{LX - MY}{L^2 + M^2}$.

Now, $LX - MY = \hat{\beta}^2 \frac{d\Phi}{d\beta^2}(\hat{\beta}^2)$ where $\Phi(z) = z^3 + z^2 \bar{Q}_1 + z \bar{Q}_2 + \bar{Q}_3$ and $z = \beta^2$.

Therefore, $\frac{d\alpha}{d\tau}(\hat{\tau}) = \frac{\hat{\beta}^2}{L^2 + M^2} \frac{d\Phi}{d\beta^2}(\hat{\beta}^2) > 0$ if $\bar{Q}_1 > 0$ and $\bar{Q}_3 > \frac{\bar{Q}_2^2}{4\bar{Q}_1} > 0$.

Since $\frac{d\alpha}{d\tau}(\hat{\tau}) > 0$, it follows that at least one eigenvalue of $\bar{D}(\lambda, \tau) = 0$ with negative real part at $\tau = 0$ will become positive for $\tau > \hat{\tau}$. The negative real part of the eigenvalue

will continue to be negative for $\tau < \hat{\tau}$. Therefore, the criterion for a Hopf bifurcation is satisfied and consequently there exists a small amplitude periodic solution as τ crosses $\hat{\tau}$.

Lemma 7.2 *If $\bar{Q}_1 > 0$, $\frac{1}{3} \left[\bar{Q}_1^2 - \left(\frac{27\bar{Q}_3 + 2\bar{Q}_1^3}{4} \right)^{\frac{2}{3}} \right] < \bar{Q}_2 < 0$ and $\bar{Q}_3 > \frac{\bar{Q}_2^2}{4\bar{Q}_1}$, then if the system (1) is stable at E^* , it remains stable for all $\tau > 0$.*

Proof We can describe criteria for the preservation of stability (instability) as follows [33, 34]:

- (1) If the polynomial $\Phi(z) = z^3 + z^2 \bar{Q}_1 + z \bar{Q}_2 + \bar{Q}_3$, where $z = \beta^2$, has no positive root, there is no change of stability.
- (2) If $\Phi(z)$ is decreasing (increasing) at all its positive roots, stability (instability) is preserved.

Now, if $\bar{Q}_1 > 0$, $\bar{Q}_2 < 0$ and $\bar{Q}_3 > \frac{\bar{Q}_2^2}{4\bar{Q}_1}$, then $\Phi(z)$ is minimum at $z_{\min} = \frac{-\bar{Q}_1 + \sqrt{\bar{Q}_1^2 - 3\bar{Q}_2}}{3}$.

Also, for the existence of $\hat{\beta} > 0$, $\Phi(z)$ must have at least one positive real root.

For this, we must have $z_{\min} > 0$. This implies $\frac{1}{3} \left[\bar{Q}_1^2 - \left(\frac{27\bar{Q}_3 + 2\bar{Q}_1^3}{4} \right)^{\frac{2}{3}} \right] < \bar{Q}_2 < 0$.

Lemma 7.3 *If E^* exists with $h > \frac{(c+y_A^*)0^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1-e_1)m_2 a_2 y_A^*}{(a_2 + y_f^*)^2} - \mu - D_1 - D_2 - r \right\}$ and $\eta > 0$, then E^* is asymptotically stable for all $\tau \in [0, \hat{\tau}_0)$.*

Proof We see that, if $\frac{1}{3} \left[\bar{Q}_1^2 - \left(\frac{27\bar{Q}_3 + 2\bar{Q}_1^3}{4} \right)^{\frac{2}{3}} \right] < \bar{Q}_2 < 0$, then $\Phi(z) = 0$ has two positive real roots, say, z_1, z_2 . Consequently, $\beta^6 + \bar{Q}_1 \beta^4 + \bar{Q}_2 \beta^2 + \bar{Q}_3 = 0$ has two positive real roots, $\beta_1 = \sqrt{z_1}, \beta_2 = \sqrt{z_2}$.

Let $\tau_k = \frac{1}{\beta_k} \arctan \left[\frac{\beta_k \{ \beta_k^4 A_{12} + \beta_k^2 (A_{11} B_{12} - A_{12} B_{11} - C_{12}) + B_{11} C_{12} - B_{12} C_{11} \}}{\beta_k^4 (B_{12} - A_{11} A_{12}) + \beta_k^2 (A_{11} C_{12} + A_{12} C_{11} - B_{11} B_{12}) - C_{11} C_{12}} \right], k = 1, 2$.

Then $\pm i\beta_k$ is a pair of imaginary roots of the equation $\bar{D}(\lambda, \tau_k) = 0, k = 1, 2$.

We define $\hat{\tau}_0 = \min \{\tau_1, \tau_2\}$.

For $h > \frac{(c+y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1-e_1)m_2 a_2 y_A^*}{(a_2 + y_f^*)^2} - \mu - D_1 - D_2 - r \right\}$ and $\eta > 0$, the system is stable at E^* for $\tau = 0$. Under these conditions, for $\tau \neq \tau_k (k = 1, 2)$, the equation $\bar{D}(\lambda, \tau) = 0$ has roots with non-zero real part and $\hat{\tau}_0$ is the minimum value of τ so that $\bar{D}(\lambda, \tau) = 0$ has purely imaginary roots.

Thus, all the roots of $\bar{D}(\lambda, \tau) = 0$ have negative real parts when $\tau \in [0, \hat{\tau}_0)$.

8 Numerical simulations

In this section, we investigate numerically, by using MATLAB, the effect of the various parameters on the qualitative behavior of the system using parameter values given in Table 1

Table 1 A default set of parameter values

Parameters	Description of	Default value	Dimension
R	Intrinsic growth rate of x	3	1/time
K	Carrying capacity	2.5	Mass/volume
m_1	Maximal growth rate of y_J on x	5	1/time
m_2	Maximal growth rate of y_A on y_J	4	1/time
a_1	Half saturation const. for uptake of x by y_J	2	Mass/volume
a_2	Half saturation const. for uptake of y_J by y_A	1	Mass/volume
e_1	Growth efficiency of y_J on x	0.5	—
e_2	Growth efficiency of y_A on y_J	0.5	—
D_1	Death rate of y_A	0.4	1/time
D_2	Death rate of y_J	0.3	1/time
$\frac{1}{\mu}$	Total time spent by y_J in its juvenile stage	0.1	Time
H	Maximal harvesting rate of y_A	0.5	1/time
C	Half saturation constant for harvesting of y_A	5	1/time
τ	Time delay due to gestation of y_A	0.5	Time

throughout, unless otherwise stated. We will verify the feasibility of the stability criterion in Section 4.

8.1 Example 1

For $\tau = 0$ and all other parameters as in Table 1, the system (2) is locally asymptotically stable at $E^* = (0.4794, 0.0458, 1.2024)$ with eigenvalues $-12.9712, -0.0496 \pm i0.8554$ (Fig. 2). We obtain $0.5 = h < c \left\{ \frac{e_1 m_1 \mu K}{(a_1 + K)(\mu + D_1)} - D_2 \right\} = 5.1774$, satisfying the analytical

Fig. 2 Time series analysis of the system (2) for $\tau = 0$ and other parameter values as given in Table 1. The system is stable at E^*

condition for persistence of the system (2) at E^* as given in Lemma 4.5 is satisfied. Also, we obtain $A = 13.0703$, $B = 2.0199$ and $C = 16.8777$ so that $AB > C$, satisfying the criterion for stability at E^* as given in Lemma 4.6.

8.2 Example 2

For $\tau = 0$ and $h = 10$ with all other parameters as in Table 1, the system (2) is locally asymptotically stable at $E_1 = (2, 0, 0)$ with eigenvalues $-3, -0.8462, -11.8538$ (Fig. 3). Also we obtain $h > c \left\{ \frac{m_1 \mu K}{(a_1 + K)(\mu + D_1)} - D_2 \right\} = 5.1774$. Therefore, the criterion for stability at E_1 as given in Lemma 4.4 is satisfied.

8.3 Effect of delay in maturation

For the parameter values as given in Table 1, the system (1) is oscillatory around E^* (Fig. 4). If the maturation delay is lowered to 0.1, the system (1) becomes locally asymptotically stable at E^* (Fig. 5).

8.4 Hopf bifurcation

8.4.1 No delay

We observe that for $m_1 = 8$ and other parameter values as in Table 1, the system (2) is oscillatory around E^* (Fig. 6). Increasing the maximal rate of harvesting, the system (2) becomes locally asymptotically stable at E^* . We therefore consider h as a bifurcation parameter. In this case, we obtain $A = 12.2113$, $B = 0.4509$ and $C = 10.9332$. Also, from

Fig. 3 Phase plane diagram of the system (2) for $\tau = 0$ and $h = 10$, other parameter values as given in Table 1 with initial values $I_1 = (3, 0.001, 0.008)$, $I_2 = (2, 0.002, 0.01)$ and $I_3 = (1.5, 0.0015, 0.006)$. The system is stable at E_1

Fig. 4 Time series analysis of the system (2) for $\tau = 0$ and $m_1 = 8$, other parameter values as given in Table 1. The system is oscillatory around E^* (dotted lines). For $m_1 = 8$, $h = 2.5$ and other parameter values as given in Table 1, the system (2) is locally asymptotically stable at E^* (solid lines)

Fig. 7a we observe that $f_1(h)$ and $f_2(h)$ intersect at $h = 1.535$, indicating that the system (2) changes its stability when the parameter h crosses the threshold $h_{cr} = 1.535$. More specifically, for $h > h_{cr}$ we see that $f_1(h) > f_2(h)$, satisfying the condition of stability at E^* as given in Lemma 4.6. For $h < h_{cr}$ we see that $f_1(h) < f_2(h)$ and so the system is unstable at E^* . Moreover, we observe that the tangent to $g(h)$ at $h = h_{cr}$ is not parallel to the h axis (Fig. 7b), satisfying the condition $\frac{dg}{dh}\big|_{(r=h_{cr})} \neq 0$ (Lemma 4.8(iii)). Thus the system

Fig. 5 Phase plane diagram of the system (1) for the parameter values as given in Table 1 with initial value I_4 . The system is oscillatory around E^*

Fig. 6 Phase plane diagram of the system (1) for $\tau = 0.1$ and all other parameter values as given in Table 1 with initial value I_4 . The system is locally asymptotically stable at E^*

(2) undergoes a subcritical Hopf bifurcation when the parameter h is increased through $h_{cr} = 1.535$.

8.4.2 Non-zero delay

It is observed that with $m_1 = 8$ and other parameter values as given in Table 1, the system (1) undergoes a subcritical Hopf bifurcation when the parameter h is increased through a

Fig. 7 (a) The relative position of $f_1(h)$, $f_2(h)$ showing that the system (2) satisfies Lemma 4.8(ii) when the two curves intersect at the $h = 1.535$. (b) The tangent to the curve $g(h) = f_1(h) - f_2(h)$ at the $h = 1.535$ is not parallel to the h axis, satisfying Lemma 4.8(iii)

Fig. 8 With $m_1 = 8$ and other parameter values as given in Table 1, the system (1) undergoes a subcritical Hopf bifurcation as h is increased through $h_{cr} = 4$

critical value $h_{cr} = 4$ (Fig. 8). This implies that a higher rate of harvesting of adult predator is required to obtain system stability at the coexistence equilibrium if the delay in maturation of predator is considered.

Also, we observe that the system (1) undergoes a supercritical Hopf bifurcation when the parameter τ is increased through a critical value $\tau_{cr} = 0.125$ (Fig. 9).

Fig. 9 The system (1) undergoes a supercritical Hopf bifurcation as τ is increased through $\tau_{cr} = 0.125$, other parameter values as given in Table 1

9 Discussion

We have considered a stage-structured model in which the adult predator exhibits cannibalism towards juveniles of its species. The adult predator is harvested with a rational harvesting policy. The main objective of this paper is to study the dynamic behavior of the system in the presence of a discrete time lag for maturation of the predator population. We have shown that solutions of the system are bounded in the long run. Firstly, we analyze the system in the absence of a time delay. It is observed that if the maximal harvesting rate of adult *Pterois volitans* exceeds a certain threshold, the system becomes locally asymptotically stable at *Pterois volitans*-free equilibrium. We have obtained conditions for permanence and the stability of the system at the coexistence equilibrium. We have also established that the system (1) remains locally asymptotically stable and all solutions approach E^* whenever the magnitude of the delay lies below some threshold value. In order to find the expression for this threshold value, we have obtained the estimated length of stability preserving delay. The stability as well as the direction of the bifurcation near the positive equilibrium E^* is obtained by applying the algorithm due to Poore. Further, numerical simulations demonstrate the following conclusions:

- (i) The system exhibits dynamic instability due to greater maturation delay.
- (ii) Increase of the maximal harvesting rate of adult *Pterois volitans* helps the system to reach stability.
- (iii) High levels of maximal uptake rate of adult *Pterois volitans* on *Parrotfish* induces oscillations around the positive equilibrium leading to dynamic instability. This represents the phenomenon of ecological imbalance due to the presence of the invasive *Pterois volitans* in a coral reef ecosystem, justifying the observations of [9] that high predation rates of adult *Pterois volitans* are detrimental to coral reef ecosystems. The dynamic instability can be controlled by increasing the maximal harvesting rate of adult *Pterois volitans*. This, too, justifies that harvesting of these species is beneficial for coral reef ecosystem as observed by [12].

Throughout the article an attempt is made to search for a suitable way to control the growth of *Parrotfish* and *Pterois volitans* and maintain stable coexistence of all the species. From analytical and numerical observations, it is seen that an increase of the harvesting of adult *Pterois volitans* induces stability of the system. Moreover, we observe that harvesting of the species at a higher rate is necessary to obtain stability of the system with the time delay than the system without delay.

Acknowledgements The paper has improved considerably, both in presentation and scientific content, by the critical comments made by the reviewers. The authors are thankful to them.

Appendix

Proof of boundedness of the system (Theorem 3.1) Let $\Sigma(t) = x(t) + y_J(t) + y_A(t)$. We have $\frac{dx}{dt} \leq rx(1 - \frac{x}{K})$, which gives $x \leq \frac{c_1 K}{c_1 + e^{-t}} \rightarrow K$ as $t \rightarrow \infty$, where c_1 is a constant.

Then for large values of t we get $\frac{d}{dt}(\Sigma(t)) \leq rK - D_0 \Sigma(t)$, where $D_0 = \min\{r, D_1, D_2\}$.

Let $u(t)$ be the solution of $\frac{du}{dt} + uD_0 = rK$, satisfying $u(0) = \Sigma(0)$. Then $u(t) = \frac{rK}{D_0} + \left(\Sigma(0) - \frac{rK}{D_0}\right)e^{-tD_0} \rightarrow \frac{rK}{D_0}$ as $t \rightarrow \infty$. By comparison, it follows that $\limsup_{t \rightarrow \infty} [x(t) + y_J(t) + y_A(t)] \leq \frac{rK}{D_0}$, proving the theorem. $\square$

Proof of Theorem 4.1 Since $\limsup_{t \rightarrow \infty} [x(t) + y_J(t) + y_A(t)] \leq \frac{rK}{D_0}$, it follows that $\limsup_{t \rightarrow \infty} [y_J(t) + y_A(t)] < \frac{rK}{D_0}$. Therefore, there exists $T_1 > 0$ such that $y_J(t) \leq M_1$ and $y_A(t) \leq M_2$, for all $t \geq T_1$ where M_1, M_2 are finite positive constants with $M_1 + M_2 < \frac{rK}{D_0}$.

For all $t \geq T_1$, we have $\frac{dx}{dt} \geq x(t) \left[r \left(1 - \frac{x(t)}{K} \right) - \frac{m_1 M_2}{a_1} \right]$.

This implies, $\frac{dx}{dt}|_{x_1} \geq 0$ for all $t \geq T_1$, where $x_1 = \frac{K(a_1 r - m_1 M_2)}{a_1 r} > 0$ and $r > \frac{m_1 M_2}{a_1}$. Also, $x \leq K$ as $t \rightarrow \infty$. Therefore, there exists $T_2 > 0$ such that $x(t) \leq K$ for all $t \geq T_2$. Therefore, for all $t \geq \max\{T_1, T_2\}$, $x_1 \leq x(t) \leq K$. Again, for all

$$\begin{aligned} t \geq \max\{T_1, T_2\}, \quad \frac{dy_J}{dt} &\geq \frac{e_1 m_1 x_1 y_A(t)}{a_1 + x_1} - (\mu + D_2) M_1 - m_2 y_A(t) \\ &> 0 \text{ if } y_A(t) > \frac{M_1(\mu + D_2)(a_1 + x_1)}{x_1(e_1 m_1 - m_2) - a_1 m_2}. \end{aligned}$$

Let there exist $y_{A_1} > 0$ such that $\frac{M_1(\mu + D_2)(a_1 + x_1)}{x_1(e_1 m_1 - m_2) - a_1 m_2} < y_{A_1} < M_2$.

Then $\frac{dy_J}{dt} > 0$ for $y_A(t) \geq y_{A_1} > 0$, for all $t > \max\{T_1, T_2\}$ and so in this case there exists $T_3 > 0$ and $0 < y_{J_1} < M_1$ such that $y_J(t) \geq y_{J_1}$ for all $t \geq T_3$.

Therefore, for all $t \geq T_3$, if $y_{A_1} \leq y_A(t) \leq M_2$, then $y_{J_1} \leq y_J(t) \leq M_1$.

Let $T = \max\{T_1, T_2, T_3\}$. Then for all $t \geq T$, there exist finite positive real numbers x_1, y_{J_1}, y_{A_1} with $x_1 = \frac{K(a_1 r - m_1 M_2)}{a_1 r}$, $y_{A_1}(t) > \frac{M_1(\mu + D_2)(a_1 + x_1)}{x_1(e_1 m_1 - m_2) - a_1 m_2}$ and $r > \frac{m_1 M_2}{a_1}$ such that $x_1 \leq x(t) \leq K$, $y_{J_1} \leq y_J(t) \leq M_1$, $y_{A_1} \leq y_A(t) \leq M_2$. $\square$

Proof of Lemma 4.2 The Jacobian of the system (2) at (x, y, z) is given by

$$J = \begin{bmatrix} r \left(1 - \frac{x}{K} \right) - \frac{m_1 a_1 y_A}{(a_1 + x)^2} & 0 & -\frac{m_1 x}{a_1 + x} \\ \frac{e_1 m_1 a_1 y_A}{(a_1 + x)^2} & -\mu - D_1 - \frac{(1 - e_2) m_2 a_2 y_A}{(a_2 + y_J)^2} & \frac{e_1 m_1 x}{a_1 + x} - \frac{(1 - e_2) m_2 y_J}{a_2 + y_J} \\ 0 & \mu & -D_2 - \frac{hc}{(c + y_A)^2} \end{bmatrix}$$

Let us consider

$$H = \begin{bmatrix} 1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$$

Then

$$J = \begin{bmatrix} r \left(1 - \frac{x}{K} \right) - \frac{m_1 a_1 y_A}{(a_1 + x)^2} & 0 & -\frac{m_1 x}{a_1 + x} \\ -\frac{e_1 m_1 a_1 y_A}{(a_1 + x)^2} & -\mu - D_1 - \frac{(1 - e_2) m_2 a_2 y_A}{(a_2 + y_J)^2} & \frac{(1 - e_2) m_2 y_J}{a_2 + y_J} - \frac{e_1 m_1 x}{a_1 + x} \\ 0 & -\mu & -D_2 - \frac{hc}{(c + y_A)^2} \end{bmatrix}$$

Then, all the off-diagonal elements of the matrix HJH are non-positive if $\frac{(1-e_2)m_2y_J}{a_2+y_J} \leq \frac{e_1m_1x}{a_1+x}$ for all t . Now, $\frac{(1-e_2)m_2y_J}{a_2+y_J} - \frac{e_1m_1x}{a_1+x} \leq 0$ if $x(t) \geq \frac{m_2(1-e_2)(1+a_1)}{e_1m_1}$, for all t . Again, if $r > \frac{m_1M_2}{a_1}$ and $K \geq \frac{a_1r\{m_2(1-e_2)(1+a_1)\}}{em_1(a_1r-m_1M_2)}$, then $x(t) \geq x_1 = \frac{K(a_1r-m_1M_2)}{a_1r} \geq \frac{m_2(1-e_2)(1+a_1)}{e_1m_1}$, for large values of t . Thus, the system (2) is competitive if $K \geq \frac{a_1r\{m_2(1-e_2)(1+a_1)\}}{em_1(a_1r-m_1M_2)}$ and $r > \frac{m_1M_2}{a_1}$. $\square$

Proof of Lemma 4.4 The variational matrix at E_1 is

$$V(E_1) = \begin{bmatrix} -r & 0 & -\frac{m_1K}{a_1+K} \\ 0 & -\mu - D_1 & \frac{e_1m_1K}{a_1+K} \\ 0 & \mu & -D_2 - \frac{h}{c} \end{bmatrix} \quad (10)$$

The characteristic equation is

$$(\lambda + r) \left\{ \lambda^2 + \lambda \left(\mu + D_1 + D_2 + \frac{h}{c} \right) + (\mu + D_1) \left(D_2 + \frac{h}{c} \right) - \frac{e_1m_1\mu K}{a_1+K} \right\} = 0$$

$$E_1 \text{ is stable if } (\mu + D_1) \left(D_2 + \frac{h}{c} \right) > \frac{e_1m_1\mu K}{a_1+K} \Rightarrow h > c \left\{ \frac{e_1m_1\mu K}{(\mu + D_1)(a_1+K)} - D_2 \right\}. \quad \square$$

Proof of Lemma 4.5. The system (2) is always unstable at E_0 .

The system (2) is unstable at E_1 if $h \leq c \left\{ \frac{e_1m_1\mu K}{(a_1+K)(\mu + D_1)} - D_2 \right\}$. Therefore, all the boundary equilibria of the system (2) are repellers if $h \leq c \left\{ \frac{e_1m_1\mu K}{(a_1+K)(\mu + D_1)} - D_2 \right\}$. Also, the system (2) is bounded. Therefore, the system is persistent at E^* if $h \leq c \left\{ \frac{e_1m_1\mu K}{(a_1+K)(\mu + D_1)} - D_2 \right\}$. $\square$

Proof of Lemma 4.6 The variational matrix at E^* is

$$V(E^*) = \begin{bmatrix} \frac{m_1z^*(a_1 + 2x^*)}{(a_1 + x^*)^2} - r & 0 & -\frac{m_1x^*}{a_1 + x^*} \\ \frac{e_1m_1a_1y_A^*}{(a_1 + x^*)^2} & -\mu - D_1 - \frac{(1-e_2)m_2a_2y_J^*}{(a_2 + y_J^*)^2} & (\mu + D_1) \frac{y_J^*}{y_A^*} \\ 0 & \mu & -D_2 - \frac{hc}{(c + y_A^*)^2} \end{bmatrix} \quad (11)$$

The characteristic equation of the variational matrix at E^* is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$ where

$$\begin{aligned} A &= \mu + D_1 + D_2 + r + \frac{hc}{(c + y_A^*)^2} + \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2}, \\ B &= \left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2} \right\} - \left\{ \frac{m_1y_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} - r \right\} \\ &\quad \times \left\{ \mu + D_1 + D_2 + \frac{(1 - e_1)m_1a_2y_A^*}{(a_2 + y_J^*)^2} + \frac{hc}{(c + y_A^*)^2} \right\} - \mu(\mu + D_1)\frac{y_J^*}{y_A^*} \text{ and} \\ C &= \left\{ r - \frac{m_1y_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \left[\left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2} \right\} \right. \\ &\quad \left. - \mu(\mu + D_1)\frac{y_J^*}{y_A^*} \right] - \frac{e_1m_1^2a_1\mu x^*y_A^*}{(a_1 + x^*)^3}. \end{aligned}$$

Now, $A > 0$ if $h > \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1y_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\}$ and $AB > C$ if $\eta > 0$, where

$$\begin{aligned} \eta &= \left\{ \mu + D_1 + D_2 + \frac{hc}{(c + y_A^*)^2} + \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2} \right\} \\ &\quad \times \left[\left\{ r^2 + D_2 + \frac{hc}{(c + y_A^*)^2} - \frac{m_1ry_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2} \right\} + \left\{ r^2 - \frac{m_1ry_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \right. \\ &\quad \left. \times \left\{ r + D_2 + \frac{hc}{(c + y_A^*)^2} - \frac{m_1y_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} - \mu(\mu + D_1)\frac{y_J^*}{y_A^*} \right] - \frac{e_1m_1^2a_1\mu x^*y_A^*}{(a_1 + x^*)^3} \end{aligned}$$

Therefore, by the Routh–Hurwitz criterion of stability, the system (2) is stable at E^* if $\eta > 0$ and $h > \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1y_A^*(a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1)m_2a_2y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\}$ hold. $\square$

Proof of Lemma 4.7 Let $p(t) = (x(t), y_J(t), y_A(t))$ be a periodic solution of the system (2).

In accordance with the criterion given by Muldowney in [25], for the asymptotic orbital stability of a periodic orbit of a general autonomous system, it is sufficient to prove that the linear system $\dot{Y}(t) = (J^{(2)}(p(t)))Y(t)$ is asymptotically stable, where $Y = [u \ v \ w]$ and $J^{(2)}$ is the second additive compound matrix of the Jacobian of the system (2).

Thus, for the solution $p(t)$, the system (2) becomes

$$\begin{aligned} \frac{du}{dt} &= \left[r \left(1 - \frac{2x}{K} \right) - \frac{m_1a_1y_A}{(a_1 + x)^2} - \mu - D_1 - \frac{(1 - e_2)m_2a_2y_A}{(a_2 + y_J)^2} \right] u \\ &\quad + \left[\frac{e_1m_1x}{a_1 + x} - \frac{(1 - e_2)m_2y_J}{a_2 + y_J} \right] v + \frac{m_1x}{a_1 + x} w \\ \frac{dv}{dt} &= \mu u + \left[r \left(1 - \frac{2x}{K} \right) - \frac{m_1a_1y_A}{(a_1 + x)^2} - D_2 - \frac{hc}{(c + y_A)^2} \right] v \\ \frac{dw}{dt} &= \frac{e_1m_1a_1y_A}{(a_1 + x)^2} v - \left[\mu + D_1 + D_2 + \frac{(1 - e_2)m_2a_2y_A}{(a_2 + y_J)^2} + \frac{hc}{(c + y_A)^2} \right] w \quad (12) \end{aligned}$$

In order to prove that the local asymptotic stability of the system (9), we shall use the following Lyapunov function $V(u(t), v(t), w(t); x(t), y_J(t), y_A(t)) = \left\| u(t), \frac{y_J(t)}{y_A(t)} v(t), \frac{y_J(t)}{y_A(t)} w(t) \right\|$, where $\|\cdot\|$ is the norm in $\mathbf{R}^3$ defined by $\|(u, v, w)\| = \sup\{|u|, |v| + |w|\}$.

Therefore, along a solution $(u(t), v(t), w(t))$ of system (9), V becomes

$$V(t) = \sup \left\{ |u(t)|, \frac{y_J(t)}{y_A(t)} (|v(t)| + |w(t)|) \right\}.$$

Let us estimate the right-derivative of V along a solution $(x(t), y_J(t), y_A(t))$ of system (2) and $(u(t), v(t), w(t))$ of system (6) where the calculations are given in [35].

$$D_+ |u(t)| \leq \left[r \left(1 - \frac{2x}{K} \right) - \frac{m_1 a_1 y_A}{(a_1 + x)^2} - \mu - D_1 - \frac{(1 - e_2) m_2 a_2 y_A}{(a_2 + y_J)^2} \right] |u| + \frac{m_1 x}{a_1 + x} (|v| + |w|) \text{ and}$$

$$\begin{aligned} D_+ (|v| + |w|) &\leq \mu |u| + \left[r \left(1 - \frac{2x}{K} \right) - D_2 - \frac{ch}{(c + y_A)^2} \right] |v| \\ &\quad - \left[\mu + D_1 + D_2 + \frac{(1 - e_2) m_2 a_2 y_A}{(a_2 + y_J)^2} + \frac{ch}{(c + y_A)^2} \right] |w|. \end{aligned}$$

$$\text{Let } \eta_1 = \max \left\{ r \left(1 - \frac{2x}{K} \right) - D_2 - \frac{ch}{(c + y_A)^2}, -\mu - D_1 - D_2 - \frac{(1 - e_2) m_2 a_2 y_A}{(a_2 + y_J)^2} - \frac{ch}{(c + y_A)^2} \right\}.$$

Then $D_+ (|v| + |w|) \leq \mu |u| + \eta_1 (|v| + |w|)$. Therefore, $D_+ \left\{ \frac{y_J}{y_A} (|v| + |w|) \right\} \leq \mu \frac{y_J}{y_A} |u| + \frac{y_J}{y_A} \left\{ \left(\frac{\dot{y}_J}{y_J} - \frac{\dot{y}_A}{y_A} \right) + \eta_1 \right\} (|v| + |w|)$. If $|u| \geq |v| + |w|$, then $D_+ V(t) \leq h_1(t) V(t)$, where $h_1(t) = r \left(1 - \frac{2x}{K} \right) - \frac{m_1 a_1 y_A}{(a_1 + x)^2} - \frac{(1 - e_2) m_2 a_2 y_A}{(a_2 + y_J)^2} + \frac{m_1 x}{a_1 + x} - \mu - D_1$. If $|u| \leq |v| + |w|$, then $D_+ V(t) \leq h_2(t) V(t)$, where $h_2(t) = \frac{e_1 m_1 x y_A}{y_J(a_1 + x)} - \frac{(1 - e_2) m_2 z}{a_2 + y_J} + \frac{h}{c + y_A} - \frac{\mu y_J}{y_A} + D_2 + \eta_1 - D_1$. Therefore, $D_+ V(t) \leq \{\eta_2(t) - D_1\} V(t)$, where $\eta_2(t) - D_1 = \max\{h_1(t), h_2(t)\}$. If the criterion for permanence hold, then $h_1(t) + D_1 \leq r + \frac{m_1}{a_1}$ for all $t > 0$ and $h_2(t) + D_1 \leq \frac{e_1 m_1 M_2}{y_{J_1}} + \frac{h}{c} + r$ for large t .

Let $M_0 = \max \left\{ r + \frac{m_1}{a_1}, h_2(t) + D_1 \leq \frac{e_1 m_1 M_2}{y_{J_1}} + \frac{h}{c} + r \right\}$. Then $\eta_2(t) \leq M_0$, for large t . Using the Gronwell inequality it follows that $V(t) \leq V(0) M_0 e^{-D_1 t}$, for large t . Therefore, $V(t) \rightarrow 0$ as $t \rightarrow \infty$. Also, if the conditions for permanence hold, the orbit of $p(t)$ remains at a positive distance form the boundary B and so for large values of t , it follows that $y_J(t), y_A(t) \geq \eta$, where $\eta = \min\{y_{J_1}, y_{A_1}\}$. Thus along the orbit $p(t)$, we have $V(t) \geq \frac{\eta D_0}{rK} \|(u, v, w)\| \geq 0$, and so $(u(t), v(t), w(t)) \rightarrow (0, 0, 0)$ as $t \rightarrow \infty$. Therefore the null solution of the system (9) is asymptotically stable and consequently the system (2) has stable periodic orbits. $\square$

Proof of Lemma 4.8 The characteristic equation of the variational matrix at E^* is $\lambda^3 + A\lambda^2 + B\lambda + C = 0$, where

$$\begin{aligned} A &= \mu + D_1 + D_2 + r + \frac{hc}{(c + y_A^*)^2} + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2}, \\ B &= \left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} - \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - r \right\} \\ &\quad \times \left\{ \mu + D_1 + D_2 + \frac{(1 - e_1) m_1 a_2 y_A^*}{(a_2 + y_J^*)^2} + \frac{hc}{(c + y_A^*)^2} \right\} - \mu (\mu + D_1) \frac{y_J^*}{y_A^*} \end{aligned}$$

and

$$C = \left\{ r - \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\} \left[\left\{ D_2 + \frac{hc}{(c + y_A^*)^2} \right\} \left\{ \mu + D_1 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} \right. \\ \left. - \mu (\mu + D_1) \frac{y_J^*}{y_A^*} \right] - \frac{e_1 m_1^2 a_1 \mu x^* y_A^*}{(a_1 + x^*)^3}.$$

The necessary and sufficient conditions for a Hopf bifurcation to occur at $h = h_{cr}$ are that

- (i) $A(h_{cr}) > 0$, $B(h_{cr}) > 0$ and $C(h_{cr}) > 0$,
- (ii) $f_1(h_{cr}) = f_2(h_{cr})$,
- (iii) $\operatorname{Re} \left[\frac{d\lambda_j(h)}{dh} \right]_{h_{cr}} \neq 0, j = 1, 2, 3$.

where $f_1(h) = A(h) B(h)$, $f_2(h) = C(h)$.

$$\text{Now, } A > 0 \quad \text{if } h > \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\}, \\ B > 0 \quad \text{if } h > \frac{(c + y_A^*)^2 \left[\mu (\mu + D_1) \frac{y_J^*}{y_A^*} + \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - D_2 - r \right\} \left\{ \mu + D_1 + D_2 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} + D_2^2 \right]}{c \left\{ \mu + D_1 + r + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\}} \quad \text{and } C > 0 \\ \text{if } h > \frac{(c + y_A^*)^2 (a_2 + y_J^*)^2}{c \left\{ (a_2 + y_J^*) (\mu + D_1) + (1 - e_1) m_2 a_2 y_A^* \right\}} \left[\left\{ \frac{e m_1^2 a \mu x^* y_A^*}{(a_1 + x^*) \{ r(a_1 + x^*)^2 - m_1 y_A^* (a_1 + 2x^*) \}} + \mu (\mu + D_1) \frac{y_J^*}{y_A^*} \right\} - D_2 \right].$$

For $h = h_{cr}$, the characteristic equation becomes $(\lambda + A)(\lambda^2 + B) = 0 \Rightarrow \lambda = -A, \pm i\sqrt{B}$.

For $h \in (h_{cr} - \epsilon, h_{cr} + \epsilon)$, the roots are in general of the form:

$$\lambda_1(h) = \beta_1(h) + i\beta_2(h), \lambda_2(h) = \beta_1(h) - i\beta_2(h), \lambda_3(h) = -A(h).$$

Therefore, $\frac{d}{dh}(\lambda^3 + A\lambda^2 + B\lambda + C) = 0$ gives $(K + iL) \frac{d\lambda}{dh} + (M + iN) = 0$, where

$$K(h) = 3\beta_1^2(h) - 3\beta_2^2(h) + 2A(h)\beta_1(h) + B(h)$$

$$L(h) = 6\beta_1(h)\beta_2(h) + 2A(h)\beta_2(h)$$

$$M(h) = C'(h) + \{\beta_1^2(h) - \beta_2^2(h)\} A'(h) + \beta_1 B'(h)$$

$$N(h) = 2\beta_1(h)\beta_2(h) A'(h) + \beta_2(h) B'(h).$$

Therefore,

$$\frac{d\lambda}{dh} = - \frac{\{M(h)K(h) + N(h)L(h)\} + i\{N(h)K(h) - M(h)L(h)\}}{K^2(h) + L^2(h)}$$

If $\{M(h)K(h) + N(h)L(h)\}_{h_{cr}} \neq 0$, then $\operatorname{Re} \left[\frac{d\lambda_i}{dh} \right]_{h=h_{cr}} \neq 0$. Therefore, if

- (i) $h_{cr} > \max\{h_0, h_1, h_2\}$,
- (ii) $f_1(h_{cr}) = f_2(h_{cr})$,
- (iii) $\{M(h)K(h) + N(h)L(h)\}_{h_{cr}} \neq 0$ all hold, where

$$\begin{aligned}
h_0 &= \frac{(c + y_A^*)^2}{c} \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \mu - D_1 - D_2 - r \right\}, \\
h_1 &= \frac{(c + y_A^*)^2 \left[\mu (\mu + D_1) \frac{y_J^*}{y_A^*} + \left\{ \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} - D_2 - r \right\} \left\{ \mu + D_1 + D_2 + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} \right\} + D_2^2 \right]}{c \left\{ \mu + D_1 + r + \frac{(1 - e_1) m_2 a_2 y_A^*}{(a_2 + y_J^*)^2} - \frac{m_1 y_A^* (a_1 + 2x^*)}{(a_1 + x^*)^2} \right\}}, \\
h_2 &= \frac{(c + y_A^*)^2 (a_2 y_J^*)^2}{c \{ (a_2 + y_J^*) (\mu + D_1) + (1 - e_1) m_2 a_2 y_A^* \}} \\
&\quad \times \left[\left\{ \frac{e m_1^2 a \mu x^* y_A^*}{(a_1 + x^*) \{ r (a_1 + x^*)^2 - m_1 y_A^* (a_1 + 2x^*) \}} + \mu (\mu + D_1) \frac{y_J^*}{y_A^*} \right\} - D_2 \right],
\end{aligned}$$

then a Hopf bifurcation occurs at $h = h_{cr}$ and also it is non-degenerate. $\square$

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