

Stage-structured Harvest Models*

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Abstract We formulate a stage-structured population model where the population is divided to two classes, the juveniles and the adults. Then, we include harvest in the model and assume that the harvesting is only on adults. The cases where the harvesting rate is constant, proportional to the number of adults, or of Holling-II type are studied. While the model dynamics are relatively simple when the harvesting rate is proportional, the model system with a constant or a Holling-II type harvesting rate can have multiple positive equilibria. We explore the existence of all possible equilibria and investigate their stability. We also give numerical examples to confirm our findings.

Keywords Stage structure, Population, Harvesting rate, Holling-II type, Stability.

MSC(2010) 34D20, 92D25, 92D40.

1. Introduction

Harvesting wildlife populations or fish populations is common commercially, economically or due to other reasons such as for nutrition, recreation or culture. It is a major component in many industries such as fisheries and natural resource managements. Obviously, it has nonnegligible ecological and economic impact on the nature and society. Investigations of effects of harvesting populations are important to environmental protection or extinction prevention of some species. Mathematical modeling of harvesting has a long history and plays an important role to help develop regulations and ecologically acceptable strategies in population dynamics [1, 2, 4, 5, 9]. It has also been applied to host-pathogen system [20] and predation where harvesting is on either prey or predator species or both [6, 8, 14, 15, 21, 22]. Moreover, various harvesting strategies with different harvesting rates have been assumed in many modeling works, including constant, proportional, periodic or impulsive rates [1, 7, 10–12, 18].

Those studies mentioned above are mostly based on homogeneous populations. They have gained insight to harvesting effects and possible optimal strategies. Successful mathematical analyses have also been achieved from those studies. Nevertheless, we note that in many harvest areas, harvesting is more selective in a

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lot of situations and for many species [3]. For example, people can only or tend to focus on certain sizes of fish. Hunting also has more particular preferences on certain size or age stages of animals. Thus, it is important to include age or size structure in modeling of harvesting. There are mathematical models formulated and studied with age or stage structure in the literature [16, 17, 19]. To carry on this direction, we consider a population that is divided into two stages, the juveniles and adults in this paper. We assume that harvesting is only on adults and that the harvesting rates are constantly in proportional to the number of the adults, or of Holling-II type. We explore the existence of all possible equilibria and investigate their stability. By using numerical examples, we confirm our analytic results. We finally give brief discussions as well.

2. In the absence of harvesting

First, we consider the following two-stage-structured population model in the absence of harvesting

$$\begin{aligned}\frac{dJ}{dt} &= B(J, A)A - (S(J, A) + D_1(J, A))J, \\ \frac{dA}{dt} &= S(J, A)J - D_2(J, A)A,\end{aligned}$$

where $J(t)$ and $A(t)$ denote the classes of juveniles and adults respectively, $B(J, A)$ is the per capita birth rate of adults, $S(J, A)$ is the per capita maturation rate of juveniles, and $D_1(J, A)$ and $D_2(J, A)$ are the per capita death rates of juveniles and adults respectively [13].

We assume that the birth rate of adults and the maturation rate of juveniles to adults are density-independent such that $B(J, A) := \beta$ and $S(J, A) := \alpha$. Then, we consider the ecological situation where food is unlimited for adults, but the presence of adults interferes food seeking for juveniles. Thus, the density dependence is negligible for adults but needs to be include for the juveniles death. Then, we let the death rates of juveniles and adults be given by $D_1(J, A) = d_0 + d_1J + d_2A$ and $D_2(J, A) = \mu_0$ respectively. Based on these assumptions, the model system becomes

$$\begin{aligned}\frac{dJ}{dt} &= \beta A - \alpha J - (d_0 + d_1J + d_2A)J, \\ \frac{dA}{dt} &= \alpha J - \mu_0 A.\end{aligned}\tag{2.1}$$

Let $N = J + A$. Then,

$$\frac{dN}{dt} = \beta A - (d_0J + \mu_0A) - (d_1J + d_2A)J \leq \beta N - \bar{d}_0N - \bar{d}_1N^2,$$

where we let

$$\bar{d}_0 := \min \{d_0, \mu_0\} \quad \text{and} \quad \bar{d}_1 := \min \{d_1, d_2\}.$$

We assume $\beta > \bar{d}_0$ and define set Ω as

$$\Omega := \left\{ (J, A); 0 \leq J + A \leq \frac{\beta - \bar{d}_0}{\bar{d}_1} \right\}.\tag{2.2}$$

Since $\frac{dJ}{dt} \geq 0$ on the A -axis and $\frac{dA}{dt} \geq 0$ on the J -axis, system (2.1) is positively invariant in set Ω . Our study is restricted in Ω hereafter.

Define the intrinsic growth rate of the population by

$$r_0 := \frac{\beta\alpha}{(\alpha + d_0)\mu_0}. \tag{2.3}$$

It is easy to check that the trivial equilibrium $E_0 = (0, 0)$ is locally asymptotically stable if $r_0 < 1$ and unstable if $r_0 > 1$. Furthermore, there exists a positive equilibrium

$$E_0^* = (J_0^*, A_0^*) = \left(J_0^*, \frac{\alpha}{\mu_0} J_0^* \right) \tag{2.4}$$

where

$$J_0^* = \frac{\mu_0(\alpha + d_0)(r_0 - 1)}{d_1\mu_0 + d_2\alpha},$$

provided $r_0 > 1$.

The Jacobian matrix of (2.1) at E_0^* has the form

$$\Lambda_0 = \begin{pmatrix} -\frac{\beta A_0^*}{J_0^*} - d_1 J_0^* \beta - d_2 J_0^* & & \\ & \alpha & -\mu_0 \end{pmatrix} = \begin{pmatrix} -\frac{\beta\alpha}{\mu_0} - d_1 J_0^* \beta - d_2 J_0^* & & \\ & \alpha & -\mu_0 \end{pmatrix}.$$

Then, we have

$$\text{tr}\Lambda_0 = -\frac{\beta\alpha}{\mu_0} - d_1 J_0^* \beta - \mu_0 < 0$$

and

$$\det \Lambda_0 = (d_1\mu_0 + d_2\alpha)J_0^* > 0.$$

Thus, E_0^* is locally asymptotically stable.

Write the right-hand side for the first and the second equation in (2.1) as f_1 and f_2 respectively. Then, we have

$$\frac{\partial f_1}{\partial J} + \frac{\partial f_2}{\partial A} = -(\alpha + d_0 + 2d_1J + d_2A) - \mu_0 < 0,$$

for all $J \geq 0$ and $A \geq 0$. Thus, the local asymptotic stability becomes global asymptotic stability for the trivial equilibrium E_0 or the positive equilibrium E_0^* if it exists.

3. Constant harvesting rate

We assume that the harvesting rate is constant in this section. The model system (2.1) becomes

$$\frac{dJ}{dt} = \beta A - \alpha J - (d_0 + d_1J + d_2A)J, \tag{3.1a}$$

$$\frac{dA}{dt} = \alpha J - \mu_0 A - H, \tag{3.1b}$$

where $H > 0$ is a constant and we assume $r_0 > 1$.

It follows from

$$\frac{dA}{dt} = \alpha J - \mu_0 A - H \leq \alpha J - \mu_0 A$$

that all trajectories of (3.1) are bounded. If there exists no positive equilibrium for (3.1), $\lim_{t \rightarrow \infty} A(t) < 0$ and thus the population goes extinct at a finite time. Then, we explore the existence of positive equilibria of system (3.1) as follows.

Setting the right hand side of (3.1b) to zero and solving for J , we have

$$J = \frac{\mu_0 A + H}{\alpha}. \quad (3.2)$$

Setting the right hand side of (3.1a) to zero and substituting (3.2) into it, we obtain

$$\beta A - (\mu_0 A + H) - \left(d_0 + \frac{d_1(\mu_0 A + H)}{\alpha} + d_2 A \right) \frac{\mu_0 A + H}{\alpha}.$$

Let

$$\begin{aligned} \Phi_c(A) &:= -((\beta - \mu_0)\alpha^2 A - \alpha^2 H - (\alpha d_0 + d_1(\mu_0 A + H) + \alpha d_2 A)(\mu_0 A + H)) \\ &= -(\beta - \mu_0)\alpha^2 A + \alpha^2 H + (\alpha d_0 + d_1 H + (d_1 \mu_0 + \alpha d_2)A)(\mu_0 A + H) \\ &= -(\beta - \mu_0)\alpha^2 A + \alpha^2 H + (d_1 \mu_0 + \alpha d_2)\mu_0 A^2 \\ &\quad + ((d_0 \alpha + d_1 H)\mu_0 + (d_1 \mu_0 + \alpha d_2)H)A + (\alpha d_0 + d_1 H)H \\ &= (d_1 \mu_0 + \alpha d_2)\mu_0 A^2 + (-(\beta - \mu_0)\alpha^2 + (d_0 \alpha + d_1 H)\mu_0 + (d_1 \mu_0 + \alpha d_2)H)A \\ &\quad + ((d_0 + \alpha)\alpha + d_1 H)H \\ &= (d_1 \mu_0 + \alpha d_2)\mu_0 A^2 - ((\beta \alpha - (d_0 + \alpha)\mu_0)\alpha - (2d_1 \mu_0 + \alpha d_2)H)A \\ &\quad + ((d_0 + \alpha)\alpha + d_1 H)H \\ &= (d_1 \mu_0 + \alpha d_2)\mu_0 A^2 - (2d_1 \mu_0 + \alpha d_2)(\hat{H} - H)A + ((d_0 + \alpha)\alpha + d_1 H)H, \end{aligned} \quad (3.3)$$

where

$$\hat{H} := \frac{(\beta \alpha - (\alpha + d_0)\mu_0)\alpha}{2d_1 \mu_0 + \alpha d_2} = \frac{(r_0 - 1)(\alpha + d_0)\alpha \mu_0}{2d_1 \mu_0 + \alpha d_2}. \quad (3.4)$$

Then, (J, A) is a positive equilibrium (3.1) if and only if A is a positive root of $\Phi_c(A) = 0$.

Clearly, if $H \geq \hat{H}$, $\Phi_c(A) = 0$ has no positive root. Suppose $H < \hat{H}$. The determinant of the quadratic equation in A in (3.3) is

$$\begin{aligned} \Delta_1(H) &:= ((\beta \alpha - (\alpha + d_0)\mu_0)\alpha - (2d_1 \mu_0 + \alpha d_2)H)^2 \\ &\quad - 4(d_1 \mu_0 + \alpha d_2)\mu_0((\alpha + d_0)\alpha + d_1 H)H \\ &= \alpha^2 (d_2^2 H^2 - 2((\beta + \mu_0)\alpha d_2 + (2\beta d_1 + d_0 d_2)\mu_0)H + (\beta \alpha - (\alpha + d_0)\mu_0)^2). \end{aligned} \quad (3.5)$$

Then, we consider the determinant of the quadratic equation in H in (3.5)

$$\begin{aligned} \Delta_2 &:= ((\beta + \mu_0)d_2 \alpha + (2\beta d_1 + d_0 d_2)\mu_0)^2 - d_2^2 ((\beta \alpha - (\alpha + d_0)\mu_0)^2) \\ &= 4\mu_0 \beta (d_1 \mu_0 + \alpha d_2)(\beta d_1 + (\alpha + d_0)d_2) > 0. \end{aligned} \quad (3.6)$$

There exist two positive roots of $\Delta_1(H) = 0$

$$H^\mp = \frac{(\beta + \mu_0)\alpha d_2 + (2\beta d_1 + d_0 d_2)\mu_0}{d_2^2} \mp \frac{\sqrt{\Delta_2}}{2d_2^2}$$

such that $\Delta_1(H) \geq 0$ if $H \leq H^-$ or $H \geq H^+$, and $\Delta_1(H) < 0$ if $H^- < H < H^+$.

Now, we show $H^- < \hat{H} < H^+$ as follows.

From (3.5), we have

$$\begin{aligned} \frac{\Delta_1(H)}{\alpha^2} &= (d_2 H - (\beta\alpha - (\alpha + d_0)\mu_0))^2 + 2d_2(\beta\alpha - (\alpha + d_0)\mu_0)H \\ &\quad - 2((\beta + \mu_0)\alpha d_2 + (2\beta d_1 + d_0 d_2)\mu_0)H \\ &= (d_2 H - (\beta\alpha - (\alpha + d_0)\mu_0))^2 - 2d_2(\alpha + d_0)\mu_0 H \\ &\quad - 2(\mu_0\alpha d_2 + (2\beta d_1 + d_0 d_2)\mu_0)H \\ &= (d_2 H - (\beta\alpha - (\alpha + d_0)\mu_0))^2 - 4(\beta d_1 + (\alpha + d_0)d_2)\mu_0 H. \end{aligned} \tag{3.7}$$

Substituting \hat{H} given in (3.4) into (3.7) then yields

$$\begin{aligned} \frac{\Delta_1(\hat{H})}{\alpha^2} &= \left(d_2 \frac{(\beta\alpha - (\alpha + d_0)\mu_0)\alpha}{2d_1\mu_0 + \alpha d_2} - (\beta\alpha - (\alpha + d_0)\mu_0) \right)^2 \\ &\quad - 4(\beta d_1 + (\alpha + d_0)d_2)\mu_0 \frac{(\beta\alpha - (\alpha + d_0)\mu_0)\alpha}{2d_1\mu_0 + \alpha d_2} \\ &= \frac{4(\beta\alpha - (\alpha + d_0)\mu_0)}{(2d_1\mu_0 + \alpha d_2)^2} \left((\beta\alpha - (\alpha + d_0)\mu_0)d_1^2\mu_0^2 \right. \\ &\quad \left. - (\beta d_1 + (\alpha + d_0)d_2)(2d_1\mu_0 + \alpha d_2)\alpha\mu_0 \right) \\ &= \frac{4(\beta\alpha - (\alpha + d_0)\mu_0)}{(2d_1\mu_0 + \alpha d_2)^2} \left(\beta\alpha d_1^2\mu_0^2 - (\alpha + d_0)d_1^2\mu_0^3 \right. \\ &\quad \left. - \beta d_1(2d_1\mu_0 + \alpha d_2)\alpha\mu_0 - (\alpha + d_0)(2d_1\mu_0 + \alpha d_2)\alpha d_2\mu_0 \right) \\ &= - \frac{4(\beta\alpha - (\alpha + d_0)\mu_0)}{(2d_1\mu_0 + \alpha d_2)^2} \left((\alpha + d_0)d_1^2\mu_0^3 \right. \\ &\quad \left. + \beta d_1(d_1\mu_0 + \alpha d_2)\alpha\mu_0 + (\alpha + d_0)(2d_1\mu_0 + \alpha d_2)\alpha d_2\mu_0 \right) < 0. \end{aligned}$$

Since $\Delta_1(H) \geq 0$ for $0 \leq H \leq H^-$ and $H^+ \leq H < \infty$, and $\Delta_1(H) < 0$ for $H^- < H < H^+$, it follows that $H^- < \hat{H} < H^+$. Thus, $\Phi_c(A) = 0$ has no positive root for $H > H^-$.

Define the harvesting threshold by

$$\bar{H}_c = \frac{(\beta + \mu_0)\alpha d_2 + (2\beta d_1 + d_0 d_2)\mu_0}{d_2^2} - \frac{\sqrt{\Delta_2}}{2d_2^2}, \tag{3.8}$$

where Δ_2 is given in (3.6). Then system has no, one or two positive equilibria if $H > \bar{H}_c$, $H = \bar{H}_c$, or $H < \bar{H}_c$, respectively.

Next, we investigate the stability of the positive equilibria.

The Jacobian matrix of system (3.1) at a positive equilibrium (J, A) has the form

$$\Lambda_1 := \begin{pmatrix} -(\alpha + d_0 + 2d_1J + d_2A) & \beta - d_2J \\ \alpha & -\mu_0 \end{pmatrix}.$$

Thus,

$$\operatorname{tr}\Lambda_1 = -(\alpha + d_0 + 2d_1J + d_2A) - \mu_0 < 0,$$

and

$$\begin{aligned} \alpha \det \Lambda_1 &= \alpha \left(\mu_0 (\alpha + d_0 + 2d_1J + d_2A) + \alpha d_2J - \beta\alpha \right) \\ &= (2d_1\mu_0 + \alpha d_2)(\mu_0 A + H) + \alpha d_2\mu_0 A - \alpha(\beta\alpha - (\alpha + d_0)\mu_0) \\ &= 2(d_1\mu_0 + \alpha d_2)\mu_0 A + (2d_1\mu_0 + \alpha d_2)H - (\alpha + d_0)\alpha\mu_0(r_0 - 1) \\ &= 2(d_1\mu_0 + \alpha d_2)\mu_0 A + (2d_1\mu_0 + \alpha d_2)(H - \hat{H}) = \Phi'_c(A). \end{aligned} \quad (3.9)$$

If there exist two positive equilibria with $A_1^c < A_2^c$ such that

$$\Phi_c(A) = (d_1\mu_0 + \alpha d_2)\mu_0 (A - A_1^c)(A - A_2^c),$$

then $\Phi'_c(A_1^c) < 0$ and $\Phi'_c(A_2^c) > 0$, and thus $\det \Lambda_1(A_1^c) < 0$ and $\det \Lambda_1(A_2^c) > 0$. Therefore, equilibrium E_1^c is unstable and E_2^c is locally asymptotically stable. We summarize our results as follows.

Theorem 3.1. *Define the harvesting threshold \bar{H}_c in (3.8). Solutions of system (3.1) go extinct at finite times if $H \geq \bar{H}_c$. If $H < \bar{H}_c$, system (3.1) has two positive equilibria $E_1^c := (J_1^c, A_1^c)$ and $E_2^c := (J_2^c, A_2^c)$ with $A_1^c < A_2^c$. Equilibrium E_1^c is unstable and E_2^c is locally asymptotically stable. Solutions either approach E_2^c or go extinct at finite times depending on initial conditions.*

We provide an example below to show the dynamics of system (3.1).

Example 3.1. Let parameters be given by

$$\beta = 8, \alpha = 0.6; d_0 = 0.4, d_1 = 0.2, d_2 = 0.3, \mu_0 = 0.3. \quad (3.10)$$

The intrinsic growth rate in the absence of harvesting is $r_0 = 16$ and the harvesting threshold is $\bar{H}_c = 4.419$. When $H = 4 < \bar{H}_c$, there are two positive equilibria $E_1^c = (9.103, 4.873)$ and $E_2^c = (14.647, 15.960)$. Equilibrium E_1^c is unstable and E_2^c is locally asymptotically stable. Solutions go across the A -axis at finite times or approach E_2^c depending on initial values as shown in the left figure in Figure 1. For $H = 7 > \bar{H}_c$, there exists no positive equilibrium and all solutions enter the fourth quadrant at finite times as shown in the right figure in Figure 1.

4. Proportional harvesting

We assume that the harvesting rate is proportional to the number of the adults in this section. Model system (2.1) then becomes

$$\begin{aligned} \frac{dJ}{dt} &= \beta A - \alpha J - (d_0 + d_1J + d_2A)J, \\ \frac{dA}{dt} &= \alpha J - \mu_0 A - hA = \alpha J - (\mu_0 + h)A, \end{aligned} \quad (4.1)$$

where $h > 0$ is constant. We assume $r_0 > 1$ so that the population survives and approaches a steady state when there is no harvesting.

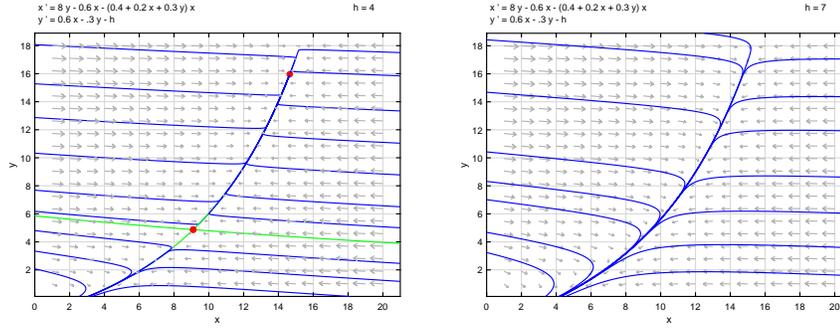


Figure 1. Parameters are given in (3.10). The harvesting threshold is $\bar{H}_c = 4.419$. For $H = 4 < \bar{H}_c$, there are two positive equilibria $E_1^c = (9.103, 4.873)$ and $E_2^c = (14.647, 15.960)$. Equilibrium E_1^c is unstable and E_2^c is locally asymptotically stable. Solutions go across the A -axis at finite times or approach E_2^c depending on their initial values as shown in the left figure. For $H = 7 > \bar{H}_c$, there exists no positive equilibrium and all solutions enter the fourth quadrant at finite times as shown in the right figure.

The new intrinsic growth rate for model system (4.1) is

$$r_0^p := \frac{\beta\alpha}{(\alpha + d_0)(\mu_0 + h)} = r_0 \frac{\mu_0}{\mu_0 + h},$$

where r_0 is given in (2.3), such that the origin is asymptotically stable if $r_0^p \leq 1$ and unstable if $r_0^p > 1$. We define a harvesting threshold for model (4.1) as

$$\bar{h}_p := (r_0 - 1)\mu_0 = \frac{\beta\alpha}{\alpha + d_0} - \mu_0. \tag{4.2}$$

Equivalently the origin of (4.1) is locally asymptotically stable if the harvesting rate $h \geq \bar{h}_p$, and is unstable if $h < \bar{h}_p$.

It is easy to check that there exists a unique positive equilibrium

$$E_p^* = \left(J_p^*, \frac{\alpha}{\mu_0 + h} J_p^* \right),$$

where

$$J_p^* = \frac{(\alpha + d_0)(\bar{h}_p - h)}{d_1\mu_0 + d_2\alpha + d_1h},$$

if and only if $h < \bar{h}_p$.

Suppose $h < \bar{h}_p$. The Jacobian matrix of (4.1) at E_p^* has the form

$$\Lambda_2 = \begin{pmatrix} -\frac{\beta\alpha}{\mu_0 + h} - d_1 J_p^* & \beta - d_2 J_p^* \\ \alpha & -(\mu_0 + h) \end{pmatrix},$$

which gives

$$\text{tr}\Lambda_2 = -\frac{\beta\alpha}{\mu_0 + h} - d_1 J_p^* - \mu_0 < 0,$$

and

$$\det \Lambda_2 = (d_1(\mu_0 + h) + d_2\alpha)J_p^* > 0.$$

Thus, E_p^* is locally asymptotically stable.

Similarly, we can show that system (4.1) has no closed orbit and thus the local asymptotic stability of the origin or positive equilibrium E_p^* implies global asymptotic stability.

5. Holling-II type harvesting rate

We next we assume that harvesting is also only on the adults and that the harvesting rate is of Holling-II type with $\frac{hA}{1+A}$ such that the harvesting rate is proportional to the number of the adults when the number of the adults is relatively small and then saturates and approaches constant h as the number of the adults is sufficiently large. System (2.1) in such a case becomes

$$\begin{aligned} \frac{dJ}{dt} &= \beta A - \alpha J - (d_0 + d_1 J + d_2 A)J, \\ \frac{dA}{dt} &= \alpha J - \mu_0 A - \frac{hA}{1+A}, \end{aligned} \quad (5.1)$$

where $h > 0$ is constant.

Model system (5.1) has the same harvesting threshold, denoted by

$$\bar{h}_f := (r_0 - 1)\mu_0.$$

Clearly, the original of (5.1) is locally asymptotically stable if $h > \bar{h}_f$ and is unstable if $h < \bar{h}_f$.

5.1. Existence of positive equilibria

We now explore the existence of positive equilibria for system (5.1) as follows.

Setting the right hand of (5.1) to zero and solving the first resulting equation for J , we have

$$J = \left(\mu_0 + \frac{h}{1+A} \right) \frac{A}{\alpha}. \quad (5.2)$$

Setting the right hand of the first equation (5.1) to zero and substituting (5.2) into it yields

$$\begin{aligned} &\beta A - \alpha J - (d_0 + d_1 J + d_2 A)J \\ &= \left(\beta - \mu_0 - \frac{h}{1+A} \right) A - \left(d_0 + d_1 \left(\mu_0 + \frac{h}{1+A} \right) \frac{A}{\alpha} + d_2 A \right) \left(\mu_0 + \frac{h}{1+A} \right) \frac{A}{\alpha} = 0. \end{aligned}$$

Equivalently, we let

$$\begin{aligned}
 \Phi_f(A) &:= \alpha^2(\beta - \mu_0) - \frac{\alpha^2 h}{1 + A} - \left(d_0 \alpha + d_1 \left(\mu_0 + \frac{h}{1 + A} \right) A + \alpha d_2 A \right) \left(\mu_0 + \frac{h}{1 + A} \right) \\
 &= \alpha^2(\beta - \mu_0) - \frac{\alpha^2 h}{1 + A} - \left(d_0 \alpha + (d_1 \mu_0 + \alpha d_2) A + \frac{d_1 A h}{1 + A} \right) \left(\mu_0 + \frac{h}{1 + A} \right) \\
 &= \alpha^2(\beta - \mu_0) - \mu_0 d_0 \alpha - \mu_0 (d_1 \mu_0 + \alpha d_2) A \\
 &\quad - \left(\alpha(\alpha + d_0) + (2d_1 \mu_0 + \alpha d_2) A + \frac{d_1 A h}{1 + A} \right) \frac{h}{1 + A} \\
 &= \mu_0 (d_1 \mu_0 + \alpha d_2) (A_0^* - A) - \left(\alpha(\alpha + d_0) + (2d_1 \mu_0 + \alpha d_2) A + \frac{d_1 A h}{1 + A} \right) \frac{h}{1 + A} \\
 &= \mu_0 (d_1 \mu_0 + \alpha d_2) (A_0^* - A) - \left(\alpha(\alpha + d_0) \right. \\
 &\quad \left. + ((\alpha(\alpha + d_0) + d_1(2\mu_0 + h) + \alpha d_2) A + (2d_1 \mu_0 + \alpha d_2) A^2) \right) \frac{h}{(1 + A)^2} \\
 &= \frac{-G(A)}{(1 + A)^2},
 \end{aligned} \tag{5.3}$$

where A_0^* is given in (2.4) and

$$G(A) := C_3 A^3 + C_2 A^2 + C_1 A + C_0$$

with

$$\begin{aligned}
 C_3 &:= (d_1 \mu_0 + \alpha d_2) \mu_0, \\
 C_2 &:= -(\beta - \mu_0) \alpha^2 + ((d_0 + 2d_2) \mu_0 + d_2 h) \alpha + 2(\mu_0 + h) d_1 \mu_0 \\
 &\quad = (\alpha + d_0) \alpha (h - \bar{h}_f) + 2(d_1 \mu_0 + \alpha d_2) \mu_0 + (2d_1 \mu_0 + (d_2 - d_0 - \alpha) \alpha) h, \\
 C_1 &:= (h - 2(\beta - \mu_0)) \alpha^2 + ((2d_0 + d_2) \mu_0 + (d_0 + d_2) h) \alpha + d_1 (\mu_0 + h)^2, \\
 &\quad = (\alpha + d_0) \alpha (h - \bar{h}_f) - (\beta - \mu_0) \alpha^2 + (d_0 \mu_0 + (\mu_0 + h) d_2) \alpha + d_1 (\mu_0 + h)^2 \\
 C_0 &:= ((h - \beta + \mu_0) \alpha + (\mu_0 + h) d_0) \alpha = (\alpha + d_0) \alpha (h - \bar{h}_f).
 \end{aligned} \tag{5.4}$$

Then, (J, A) is a positive equilibrium of system (5.1) if and only if the component A satisfies $\Phi_f(A) = 0$ or $G(A) = 0$. Clearly, the existence of positive equilibria depends on the harvesting rate.

5.1.1. The case of $h \geq \bar{h}_f$

Notice that $C_3 > 0$ in (5.4) for all parameter settings. Then, if $h \geq \bar{h}_f$, $C_0 = G(0) \geq 0$ and thus $G(A) = 0$ has at most two positive roots from Descartes' Rule of Signs.

We first consider the case of $h = \bar{h}_f$. Then, $C_0 = 0$ and

$$G(A) = A(C_3 A^2 + D_2 A + D_1) \tag{5.5}$$

where

$$\begin{aligned}
 D_2 &:= 2(d_1 \mu_0 + \alpha d_2) \mu_0 + (2d_1 \mu_0 + (d_2 - d_0 - \alpha) \alpha) \bar{h}_f, \\
 D_1 &:= -(\beta - \mu_0) \alpha^2 + (d_0 \mu_0 + (\mu_0 + \bar{h}_f) d_2) \alpha + d_1 (\mu_0 + \bar{h}_f)^2.
 \end{aligned} \tag{5.6}$$

Since $\mu_0 + \bar{h}_f = \mu_0 r_0$,

$$\begin{aligned} D_1 &= \mu_0 \alpha (\alpha + d_0) + \mu_0 r_0 (d_1 \mu_0 r_0 + \alpha d_2) - \beta \alpha^2 \\ &= \mu_0 \alpha (\alpha + d_0) + \frac{\beta \alpha}{\alpha + d_0} \left(\frac{\beta \alpha d_1}{\alpha + d_0} + \alpha d_2 \right) - \beta \alpha^2 > 0, \end{aligned}$$

provided

$$\frac{\mu_0 (\alpha + d_0)}{\beta \alpha} + \frac{1}{\alpha + d_0} \left(\frac{\beta d_1}{\alpha + d_0} + d_2 \right) > 1. \quad (\text{H3})$$

If $D_2 \geq 0$ and (H3) holds so that $D_1 > 0$, then $G(A) > 0$ and has no positive root.

Suppose (H3) holds and $D_2 < 0$. We write the discriminant of the quadratic equation in (5.5) as

$$\Delta_1 := D_2^2 - 4D_1 C_3.$$

Then, it is clear that $G(A)$ has no positive root if $\Delta_1 < 0$, and a unique positive root $A^* = -\frac{D_2}{2C_3}$ if $\Delta_1 = 0$, which implies a unique positive equilibrium of system (5.1).

If $\Delta_1 > 0$, then $G(A)$ has two positive roots $A_1^{**} = -\frac{D_2 + \sqrt{\Delta_1}}{2C_3} < A_2^{**} = -\frac{D_2 - \sqrt{\Delta_1}}{2C_3}$ and so there are two positive equilibria of (5.1).

For the case of $h > \bar{h}_f$, we assume condition (H3) holds so that $C_1 > 0$. Clearly if $C_2 \geq 0$, $G(A) > 0$ and has no positive root. Then, we assume $C_2 < 0$ and consider

$$G'(A) = 3C_3 A^2 + 2C_2 A + C_1.$$

Write its discriminant as

$$\Delta_2 := C_2^2 - 3C_1 C_3.$$

If $\Delta_2 < 0$, $G(A)$ has no positive critical point and if $\Delta_2 = 0$ it has one positive critical point. In either case, since $G(0) > 0$ and $G'(0) = C_1 > 0$, $G(A) > 0$ for all $A \geq 0$ and then system (5.1) has no positive equilibrium.

Assume $\Delta_2 > 0$. Then, $G'(A) = 0$ has two positive roots

$$A^\mp = \frac{-C_2 \mp \sqrt{\Delta_2}}{3C_3}.$$

Again, since $G(0) > 0$ and $G'(0) = C_1 > 0$, $G(A^-) > 0$. Then, if $G(A^+) > 0$, $G(A)$ has no positive root and if $G(A^+) = 0$, A^+ is the unique positive root of $G(A)$ which implies (5.1) has a unique positive equilibrium (J, A) with $A = A^+$.

On the other hand, if $G(A^+) < 0$, $G(A)$ has two positive roots $A_1^{**} < A^+ < A_2^{**}$. Then (5.1) has two positive equilibria (J_1^{**}, A_1^{**}) and (J_2^{**}, A_2^{**}) .

5.1.2. The case of $h < \bar{h}_f$

We now consider the case where $h < \bar{h}_f$. We still have $C_3 > 0$ but $C_0 = G(0) < 0$. Thus, $G(A) = 0$ has at least one positive root. If $C_1 \leq 0$, or $C_2 \geq 0$, it follows from Descartes' Rule of Signs, $G(A)$ has a unique positive root. Then, we assume $C_1 > 0$ and $C_2 < 0$.

If $\Delta_2 < 0$, $G'(A)$ has no critical point and if $\Delta_2 = 0$, $G'(A)$ has one repeated critical point. In either case, $G(A)$ is monotone increasing. Hence, $G(A)$ has a unique positive root.

Suppose $\Delta_2 > 0$. Then, $G'(A) = 0$ has two positive roots

$$0 < \bar{A}_1 := \frac{-C_2 - \sqrt{\Delta_2}}{3C_3} < \bar{A}_2 := \frac{-C_2 + \sqrt{\Delta_2}}{3C_3}. \tag{5.7}$$

It is easy to check that polynomial $G(A) = 0$ has a unique positive root if $G(\bar{A}_2) > 0$, two positive roots if $G(\bar{A}_1) = 0$ or $G(\bar{A}_2) = 0$, and three positive roots if $G(\bar{A}_1) > 0$ and $G(\bar{A}_2) < 0$.

We summarize the existence of the positive equilibria in Table 1.

Table 1. Summary of the numbers of positive equilibria of system (5.1).

$h = \bar{h}_f$				$h > \bar{h}_f$				
$D_2 \geq 0$	$D_2 < 0$			$C_2 \geq 0$	$\Delta_2 \leq 0$	$C_2 < 0$		
	$\Delta_1 < 0$	$\Delta_1 = 0$	$\Delta_1 > 0$			$\Delta_2 > 0$		
						$G(A^*) > 0$	$G(A^*) = 0$	$G(A^*) < 0$
0	0	1	2	0	0	0	1	2

$h < \bar{h}_f$				
$C_1 \leq 0$ or $C_2 \geq 0$	$C_1 > 0$ and $C_2 < 0$			
	$\Delta_2 \leq 0$	$\Delta_2 > 0$		
		$G(\bar{A}_2) > 0$	$G(\bar{A}_1) = 0$ or $G(\bar{A}_2) = 0$	$G(\bar{A}_1) > 0$ and $G(\bar{A}_2) < 0$
1	1	1	2	3

In Table 1, $\bar{h}_f = (r_0 - 1)\mu_0$, $C_i, i = 1, 2, 3$, are given in (5.4), $D_i, i = 1, 2$, are given in (5.6), $A^* = -\frac{D_2}{2C_3}$, and $\bar{A}_i, i = 1, 2$, are given in (5.7). The last row is the numbers of positive equilibria for different cases.

Remark 5.1. From Table 1, we note that if $C_2 \geq 0$, system (5.1) has either no positive or a unique equilibrium; that is, it has no multiple positive equilibria and its dynamics are relatively simple, no matter $h \geq \bar{h}_f$ or $h < \bar{h}_f$.

It follows from (5.4) that

$$\begin{aligned} C_2 &= (2d_1\mu_0 + \alpha d_2)h - (\beta - \mu_0)\alpha^2 + (d_0 + 2d_2)\mu_0\alpha + 2d_1\mu_0^2 \\ &= (2d_1\mu_0 + \alpha d_2)h - (((\beta - \mu_0)\alpha - d_0\mu_0)\alpha - 2(d_1\mu_0 + \alpha d_2)\mu_0) \\ &= (2d_1\mu_0 + \alpha d_2)h - \left(\bar{h}_f - 2\frac{(d_1\mu_0 + \alpha d_2)\mu_0}{(d_0 + \alpha)\alpha} \right) (\alpha + d_0)\alpha. \end{aligned}$$

If we write

$$\hat{h} := 2\frac{(d_1\mu_0 + \alpha d_2)\mu_0}{(d_0 + \alpha)\alpha}, \tag{5.8}$$

then $C_2 \geq 0$ if

$$\bar{h}_f \leq \hat{h},$$

or

$$\begin{cases} \bar{h}_f \geq \hat{h} \text{ and} \\ h \geq (\bar{h}_f - \hat{h}) \frac{(\alpha + d_0)\alpha}{2d_1\mu_0 + \alpha d_2}. \end{cases}$$

Otherwise, if

$$\begin{cases} \bar{h}_f \geq \hat{h} \text{ and} \\ h < (\bar{h}_f - \hat{h}) \frac{(\alpha + d_0)\alpha}{2d_1\mu_0 + \alpha d_2}, \end{cases}$$

or

$$\begin{cases} \bar{h}_f > \hat{h} \text{ and} \\ h \leq (\bar{h}_f - \hat{h}) \frac{(\alpha + d_0)\alpha}{2d_1\mu_0 + \alpha d_2}, \end{cases}$$

then $C_2 < 0$.

5.2. Stability of equilibria

We investigate the local stability of the positive equilibria in this section.

The Jacobian matrix at a positive equilibrium has the form

$$\Lambda_3 := \begin{pmatrix} -\frac{\beta A}{J} - d_1 J & \beta - d_2 J \\ \alpha & -\mu_0 - \frac{h}{(1+A)^2} \end{pmatrix} = \begin{pmatrix} -\frac{\beta A}{J} - d_1 J & \beta - d_2 J \\ \alpha & -\frac{\alpha J}{A} + \frac{hA}{(1+A)^2} \end{pmatrix}.$$

The trace of Λ_3

$$\text{tr}\Lambda_3 = -\frac{\beta A}{J} - d_1 J - \mu_0 - \frac{h}{(1+A)^2}$$

is negative. Thus, the local stability of a positive equilibrium is determined by the determinant of Λ_3

$$\begin{aligned} \det \Lambda_3 &= \left(\frac{\beta A}{J} + d_1 J \right) \left(\frac{\alpha J}{A} - \frac{hA}{(1+A)^2} \right) - \alpha(\beta - d_2 J) \\ &= \frac{\alpha J}{A} (d_1 J + d_2 A) - \frac{hA}{(1+A)^2 J} (d_1 J^2 + \beta A) \\ &= \left(\mu_0 + \frac{h}{1+A} \right) (d_1 J + d_2 A) - \frac{hA}{(1+A)^2 J} (d_1 J^2 + \beta A) \\ &= \mu_0 (d_2 A + d_1 J) + \frac{h}{(1+A)^2 J} (d_1 J^2 (1+A) + d_2 J A (1+A) - d_1 J^2 A - \beta A^2) \\ &= \mu_0 d_2 A + \mu_0 d_1 \frac{A}{\alpha} \left(\mu_0 + \frac{h}{1+A} \right) + \frac{h}{(1+A)^2} (d_1 J + d_2 A - A(\alpha + d_0 + d_1 J)), \end{aligned}$$

and then

$$\begin{aligned} \frac{\alpha}{A} \det \Lambda_3 &= \mu_0(d_1\mu_0 + \alpha d_2) + d_1\mu_0 \frac{h}{1+A} \\ &\quad + \frac{h}{(1+A)^2} \left(d_1(1-A) \left(\mu_0 + \frac{h}{1+A} \right) + \alpha(d_2 - \alpha - d_0) \right) \\ &= \mu_0(d_1\mu_0 + \alpha d_2) + \frac{h}{(1+A)^2} \left(2d_1\mu_0 + d_1(1-A) \frac{h}{1+A} + \alpha(d_2 - \alpha - d_0) \right) \\ &= \mu_0(d_1\mu_0 + \alpha d_2) \\ &\quad + \frac{h}{(1+A)^3} (2d_1\mu_0(1+A) + d_1(1-A)h + \alpha(d_2 - \alpha - d_0)(1+A)) \\ &= \mu_0(d_1\mu_0 + \alpha d_2) + \frac{h}{(1+A)^3} ((\alpha(d_2 - \alpha - d_0) \\ &\quad + d_1(2\mu_0 - h))A + \alpha(d_2 - \alpha - d_0) + d_1(h + 2\mu_0)). \end{aligned}$$

On the other hand, it follows from (5.3) that

$$\begin{aligned} \Phi'_f(A) &= -\mu_0(d_1\mu_0 + \alpha d_2) - ((d_1(2\mu_0 - h) + \alpha(d_2 - d_0 - \alpha))A \\ &\quad + d_1(2\mu_0 + h) + \alpha(d_2 - d_0 - \alpha)) \frac{h}{(1+A)^3}, \end{aligned}$$

and hence

$$\det \Lambda_3 = -\frac{A}{\alpha} \Phi'_f(A) = \frac{AG'(A)}{\alpha(1+A)^2}$$

at the positive equilibrium.

Notice that in the case of $h \geq \bar{h}_f$, if there exists a unique positive equilibrium, its A component is not a simple root of $G(A) = 0$. Thus, it is not a hyperbolic equilibrium. However, it happens rare in a real ecological situation. Then, we ignore such a special case and draw our conclusions of the local stability for all hyperbolic positive equilibria of system (5.1) as follows.

- If system (5.1) has only one positive equilibrium $E^* = (J^*, A^*)$ which is hyperbolic, then

$$G(A) = K_1(A)(A - E^*),$$

where $K_1(A) > 0$. Thus, $G'(A^*) > 0$ and then $\det \Lambda_3(E^*) > 0$, which implies that E^* is locally asymptotically stable.

- If system (5.1) has two positive equilibria $E_1^{**} = (J_1^{**}, A_1^{**})$ and $E_2^{**} = (J_2^{**}, A_2^{**})$ with $A_1^{**} < A_2^{**}$, then

$$G(A) = K_2(A)(A - A_1^{**})(A - A_2^{**}),$$

where $K_2(A) > 0$. Thus, $G'(A_1^{**}) < 0$ and $G'(A_2^{**}) > 0$, and then $\det \Lambda_3(E_1^{**}) < 0$ and $\det \Lambda_3(E_2^{**}) > 0$. Therefore, E_1^{**} is unstable and E_2^{**} is locally asymptotically stable.

- If system (5.1) has three positive equilibria $E_1^{***} = (J_1^{***}, A_1^{***})$, $E_2^{***} = (J_2^{***}, A_2^{***})$, and $E_3^{***} = (J_3^{***}, A_3^{***})$ with $A_1^{***} < A_2^{***} < A_3^{***}$, then

$$G(A) = C_3(A - A_1^{***})(A - A_2^{***})(A - A_3^{***})$$

with $C_3 > 0$. Thus, $G'(A_1^{***}) > 0$, $G'(A_2^{***}) < 0$, and $G'(A_3^{***}) > 0$, and hence $\det \Lambda_3(E_1^{***}) > 0$, $\det \Lambda_3(E_2^{***}) < 0$, and $\det \Lambda_3(E_3^{***}) > 0$. As a result, E_2^{***} is unstable and E_1^{***} and E_3^{***} are both locally asymptotically stable.

We provide an example to demonstrate our results in Example 5.1. Since the dynamics of system (5.1) are relatively simple without multiple positive equilibria if $C_2 \geq 0$, we focus on the parameter settings which lead to $C_2 < 0$.

Example 5.1. Let parameters be given by

$$\beta = 8, \alpha = 0.6; d_0 = 0.4, d_1 = 0.2, d_2 = 0.3, \mu_0 = 0.3. \quad (5.9)$$

Then, the intrinsic growth rate in the absence of harvesting is $r_0 = 16$, the harvesting threshold is $\bar{h}_f = 4.5$, and $\hat{h} = 0.24 < \bar{h}_f$ such that $C_2 < 0$ for all $h \leq (\bar{h}_f - \hat{h}) \frac{(\alpha + d_0)\alpha}{2d_1\mu_0 + \alpha d_2} = 6.086$. Next, we let the harvest start and gradually increase the harvesting rates with 3 and $4 < \bar{h}_f$, and 4.7 and $5 > \bar{h}_f$, respectively, all less than 6.086.

When $h = 3$, $C_0 = -0.900$, $C_1 = -0.828$, $C_2 = -1.656$, and $C_3 = 0.072$. There exists a unique positive equilibrium $E^* = (16.552, 23.512)$ which is locally asymptotically stable. Indeed, since it is the only positive equilibrium and the trivial equilibrium $(0, 0)$ is unstable, the stability is also global. The solution orbits are shown in the upper left figure in Figure 2.

When $h = 4 < \bar{h}_f$, C_0 is still negative, but $C_1 = 1.472 > 0$ and $C_2 = -1.356 < 0$. Since $C_3 = 0.072$ and now $\Delta_2 := 0.981 > 0$, there exist two positive critical points of $G(A)$: $\bar{A}_1 = 0.511$ and $\bar{A}_2 = 5.952$. Then, it follows from $G(\bar{A}_1) = 0.143 > 0$ and $G(\bar{A}_2) = -7.018 < 0$ that three positive equilibria $E_1^{***} = (1.552, 0.270)$, $E_2^{***} = (3.542, 0.872)$, and $E_3^{***} = (15.155, 17.691)$ exist. Equilibria E_1^{***} and E_3^{***} are locally asymptotically stable, and E_2^{***} is unstable as shown in the upper right figure in Figure 2.

For $h = 4.7 > \bar{h}_f$, the trivial equilibrium $(0, 0)$ is locally asymptotically stable. In this case, $C_0 = 0.120 > 0$, $C_1 = 3.332$, and $C_2 = -1.146$. Since $\Delta_2 = 1.357 > 0$, there are two positive equilibria $E_1^{**} = (8.152, 3.861)$ and $E_2^{**} = (13.281, 12.092)$. Equilibrium E_1^{**} is a unstable and E_2^{**} is locally asymptotically stable as shown in the lower left figure in Figure 2.

We finally let $h = 5 > \bar{h}_f$. Since now $C_2 = -1.056$ and $\Delta_2 = -0.086 < 0$, there exists no positive equilibrium and the trivial equilibrium is globally asymptotically stable as shown in the lower right figure in Figure 2.

6. Concluding remarks

In this paper, we formulated a simple stage-structured harvesting population model composed of juveniles and adults where the harvesting is only on adults. We considered three different cases where the harvesting rate is constant, proportional to the number of the adults, or of Holling-II type.

In the absence of harvesting, the model dynamics are simple that the population either goes extinct or approaches a positive steady state, regardless of their initial values, if the intrinsic growth rate is less than or greater than one. When harvesting is introduced into the model, we define a harvesting threshold for each of the three cases. The asymptotic behavior of the solutions is determined by how the

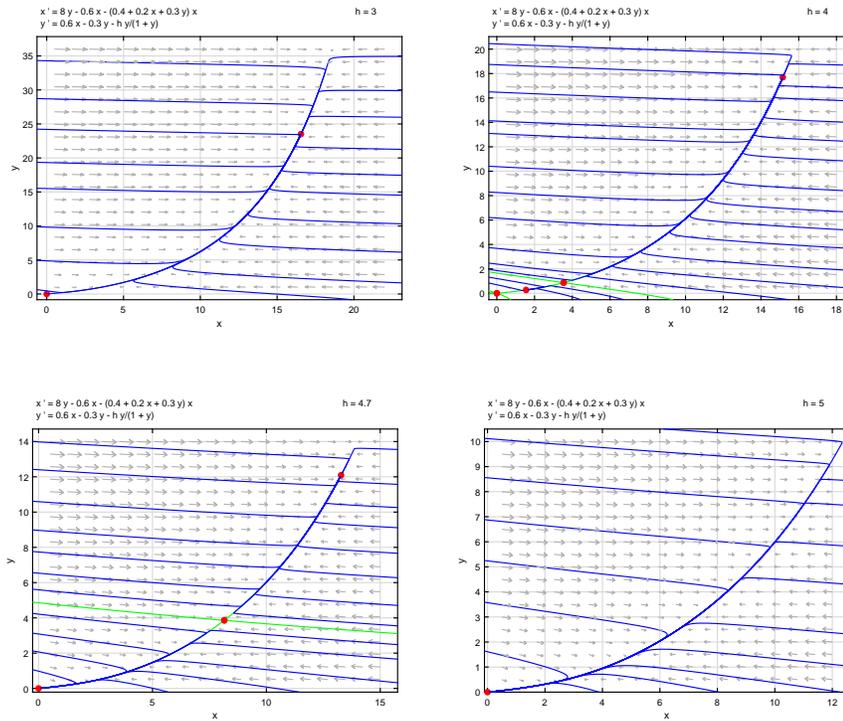


Figure 2. With parameters given in (5.9), the harvesting threshold is $\bar{h}_f = 4.5$, and $\hat{h} = 0.24$, given in (5.8), is less than \bar{h}_f so that $C_2 < 0$ for all $h \geq 0$. When $h = 3 < \bar{h}_f$, there is a unique positive equilibrium $E^* = (16.552, 23.512)$ which is globally asymptotically stable as shown in the upper left figure. When $h = 4$ still less than \bar{h}_f , there exist three positive equilibria $E_1^{***} = (1.552, 0.270)$, $E_2^{***} = (3.542, 0.872)$, and $E_3^{***} = (15.155, 17.691)$, where E_1^{***} and E_3^{***} are locally asymptotically stable, and E_2^{***} is unstable, as shown in the upper right figure. As $h = 4.7 > \bar{h}_f$, there are two positive equilibria $E_1^{**} = (8.152, 3.861)$ and $E_2^{**} = (13.281, 12.092)$ where E_1^{**} is unstable and E_2^{**} is locally asymptotically stable. The origin is also locally asymptotically stable as shown in the lower left figure. For $h = 5 > \bar{h}_f$, no positive equilibrium exists and the origin is globally asymptotically stable as shown in the lower right figure.

harvesting rate is related to the harvesting threshold. When the harvesting rate is constant, system (3.1) has two positive equilibria and the population goes extinct at finite times or survives and approaches to a locally asymptotically stable positive equilibrium if the harvesting rate H is less than the threshold \bar{H}_c given in (3.8). The population goes extinct at finite times with all initial values if the harvesting rate H is greater than the threshold \bar{H}_c .

If the harvesting rate is proportional to the number of the adults, the dynamics are relatively simple. Based on the harvesting threshold \bar{h}_p defined in (4.2), system (4.1) has no positive equilibrium and the trivial solution is globally asymptotically stable if the harvesting rate $h \geq \bar{h}_p$. There exists a unique positive equilibrium which is globally asymptotically stable and the trivial equilibrium is unstable if $h < \bar{h}_p$.

The dynamics with the Holling-II type harvesting rate is relatively more complicated. We also defined threshold \bar{h}_f with which the origin is locally asymptotically

stable if $h > \bar{h}_f$ and unstable if $h < \bar{h}_f$. Moreover, system (5.1) has at most two, possibly no, one, or two positive equilibria if $h \geq \bar{h}_f$. If the positive equilibrium is unique, it is nonhyperbolic and unstable. System (5.1) has at least one, possibly one, two or three positive equilibria if $h < \bar{h}_f$. If there is only one hyperbolic positive equilibrium, it is always globally asymptotically stable and the origin is unstable. If there are two positive equilibria, the one with larger component A and the origin are both locally asymptotically stable and the positive equilibrium with smaller component A is unstable. In the case where there are three positive equilibria with positive components $A_1^{***} < A_2^{***} < A_3^{***}$, the two positive equilibria with components A_1^{***} and A_3^{***} are locally asymptotically stable and the origin and the positive equilibrium with component A_2^{***} are unstable.

For system (5.1), when the harvesting exceeds the harvesting threshold, the population does not necessarily go extinct and can still survive depending on its initial size. This may contribute to the Holling-II type harvesting rate which saturates as the number of the adults becoming sufficiently large and has a upper limit. When the harvesting is less than the harvesting threshold, on the other hand, the population, instead of approaching a unique steady state, may survive at two different levels, also depending on its initial size. To better protect the environment or prevent extinction of some species, it is therefore important to set necessary regulations and to investigate the effects of different harvesting strategies. The study in this paper may provide a helpful guidance to that as well.

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