SIAM J. APPL. MATH.
Vol. 73, No. 5, pp. 1876–1905

BIFURCATIONS OF INVARIANT TORI IN PREDATOR-PREY MODELS WITH SEASONAL PREY HARVESTING*

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Abstract. In this paper we study bifurcations in predator-prey systems with seasonal prey harvesting. First, when the seasonal harvesting reduces to constant yield, it is shown that various kinds of bifurcations, including saddle-node bifurcation, degenerate Hopf bifurcation, and Bogdanov–Takens bifurcation (i.e., cusp bifurcation of codimension 2), occur in the model as parameters vary. The existence of two limit cycles and a homoclinic loop is established. Bifurcation diagrams and phase portraits of the model are also given by numerical simulations, which reveal far richer dynamics compared to the case without harvesting. Second, when harvesting is seasonal (described by a periodic function), sufficient conditions for the existence of an asymptotically stable periodic solution and bifurcation of a stable periodic orbit into a stable invariant torus of the model are given. Numerical simulations, including bifurcation diagrams, phase portraits, and attractors of Poincaré maps, are carried out to demonstrate the existence of bifurcation of a stable periodic orbit into an invariant torus and bifurcation of a stable homoclinic loop into an invariant homoclinic torus, respectively, as the amplitude of seasonal harvesting increases. Our study indicates that to have persistence of the interacting species with seasonal harvesting in the form of asymptotically stable periodic solutions or stable quasi-periodic solutions, initial species densities should be located in the attraction basin of the hyperbolic stable equilibrium, stable limit cycle, or stable homoclinic loop, respectively, for the model with no harvesting or with constant-yield harvesting. Our study also demonstrates that the dynamical behaviors of the model are very sensitive to the constant-yield or seasonal prey harvesting, and careful management of resources and harvesting policies is required in the applied conservation and renewable resource contexts.

Key words. predator-prey model, seasonal harvesting, Bogdanov–Takens bifurcation, degenerate Hopf bifurcation, periodic orbit, invariant torus, homoclinic torus

AMS subject classifications. Primary, 34C23, 34C25; Secondary, 37G15, 92D25

DOI. 10.1137/120895858

1. Introduction.

Understanding the nonlinear dynamics of predator-prey systems with harvesting is very important and useful in studying the management of renewable resources, since predation is one of the most fundamental interactions within a biological system and harvesting is commonly practiced in fishery, forestry, and wildlife management (Clark [12], Chrstensen [11], Hill et al. [18]). In the last three decades, great attention has been paid to investigating the effect of harvesting on the dynamics of predator-prey systems and the role of harvesting in the management of renewable resources; see Beddington and Cooke [1], Beddington and May [2], Brauer and Soudack [7, 8, 9], Dai and Tang [14], Etoua and Rousseau [15], Hogarth et al. [20], Huang, Gong, and Ruan [22], Leard, Lewis, and Rebaza [26], May et al. [27], Myerscough et al. [28], and Xiao and Ruan [38]. Mathematically, it is very important

*Received by the editors October 22, 2012; accepted for publication (in revised form) July 1, 2013; published electronically October 22, 2013.
http://www.siam.org/journals/siap/73-5/89585.html

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to study various possible bifurcations in a predator-prey system when it is perturbed by the harvesting effort. Ecologically and economically, it is crucial to exploit biological resources with maximum sustainable yield (MSY) while maintaining the survival of all interacting populations. If the harvesting of a population exceeds its MSY (i.e., the population is overexploited), then this population will become extinct.

Two types of harvesting regimes, *constant-effort harvesting*, described by a constant multiplication of the size of the population under harvest, and *constant-yield harvesting*, described by a constant independent of the size of the population under harvest, have been proposed to qualitatively describe the effect of harvest (May et al. [27]). However, harvesting does not always occur with constant yield or constant effort. For example, many species of fish are harvested at a higher rate in warmer seasons than in colder months (Hirsch, Smale, and Devaney [19]). Temporal periodically harvested area closures have been employed across the Indo-Pacific for centuries and are a common measure within contemporary community-based and comanagement frameworks (Cohen and Foale [13]). Polovina, Abecassis, and Howell [30] examined trends in the deep-set fishery using daily logbook data submitted to the National Marine Fisheries Service (NMFS) by longline vessel captains and plotted the number of hooks deployed in the deep-set sector of the Hawaii longline fishery during 1996–2006, showing seasonal patterns in fishing effort (see Figure 1.1). So it is more reasonable to assume that the population is harvested at a periodic rate, corresponding to seasonal harvesting such as seasonal open hunting or fishing seasons (Brauer and Sánchez [6]), which has received little attention. In [19], Hirsch, Smale, and Devaney considered a single species with logistic growth and periodic harvesting and discussed the existence and the number of periodic orbits by calculating the Poincaré map. In [6], Brauer and Sánchez considered autonomous single population models under periodic harvesting and sought conditions under which there is an asymptotically stable periodic solution. However, little is known about periodic harvesting of interacting populations, and this is a topic with many interesting questions to be explored [6].

Group defense is a phenomenon in population dynamics in which predation by predators decreases when the density of the prey population is sufficiently large, which is also related to the nutrient uptake inhibition phenomenon in chemical kinetics. Nonlinear dynamics of predator-prey systems with group defense have been investi-

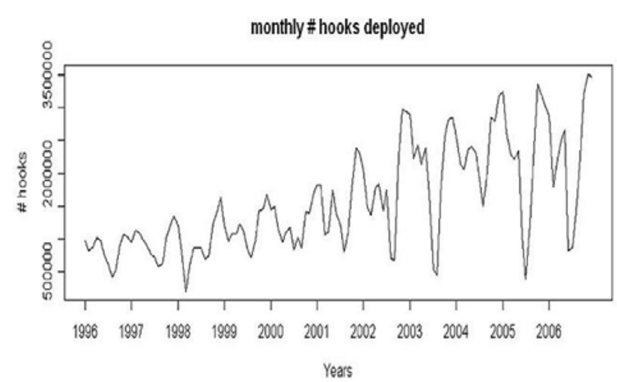

Fig. 1.1. *Monthly data on the number of hooks deployed in the deep-set sector of the Hawaii longline fishery during* 1996–2006 *(from Polovina, Abecassis, and Howell* [30]*, courtesy of the National Oceanic and Atmospheric Administration (NOAA) and the Department of Commerce).*

gated extensively; see Freedman and Wolkowicz [17], Wolkowicz [37], Ruan and Xiao [33], and Zhu, Campbell, and Wolkowicz [42]. A nonmonotone functional response function

$$p_1(x) = \frac{mx}{a + x^2}$$

(based on the Holling type II function $\frac{mx}{a+x}$) has been used to describe group defense, where $m > 0$ denotes the maximal growth rate of the species and $a > 0$ is the half-saturation constant. Very interesting bifurcations, including saddle-node bifurcation, Hopf bifurcation, homoclinic bifurcation, and Bogdanov–Takens bifurcation, have been observed (see Ruan and Xiao [33]). Based on the Ivlev functional response function $\alpha(1 - e^{-\beta x})$, another nonmonotone functional response function

$$p_2(x) = \alpha x e^{-\beta x}$$

was also introduced (Ruan and Freedman [32], Freedman and Ruan [16]), where $\alpha > 0$ is the grazing rate of predators and $\beta > 0$ is the reciprocal of the density of the prey at which predation reaches its maximum and starts to decrease (see Figure 2.1). Note that the study of a predator-prey model with functional response function $p_2(x)$ is more challenging than that with $p_1(x)$ since the interior equilibria cannot be expressed explicitly. Nevertheless, Xiao and Ruan [39] studied such a model, that is, system (1.1) with $h_0 = 0$ and $\gamma_0 = 0$, and showed that similar bifurcations occur in the model.

Roughly speaking, the bifurcations in predator-prey models with group defense (i.e., with nonmonotone functional response) demonstrate that predators are more likely to be driven into extinction when the density of the prey population is sufficiently large. One approach to maintaining the persistence of the system is to introduce a top predator that will predate both species (Ruan and Freedman [32]). In this paper we explore the possibility of having coexistence of both species by harvesting the abundant prey population. For this purpose, we consider the following predator-prey system with group defense and seasonal prey harvesting:

$$\begin{aligned} \dot{x} &= rx(1 - \tfrac{x}{K}) - \alpha x y e^{-\beta x} - (h_0 + \gamma_0 \sin(2\pi t)), \\ \dot{y} &= y(\mu \alpha x e^{-\beta x} - D), \end{aligned} \tag{1.1}$$

where x and y are functions of time representing population densities of the prey and predators, respectively, $r > 0$ represents the intrinsic growth rate of the prey in absence of predators, $K > 0$ denotes the carrying capacity of the prey population, $D > 0$ is the death rate of predators, $\mu > 0$ is the maximal conversion rate of the prey into the growth of predators, and $h_0 + \gamma_0 \sin(2\pi t)$ describes the seasonal harvesting effort on the prey population, in which $h_0 > 0$ is the constant-yield harvesting rate and $\gamma_0 \geq 0$ is the amplitude of the seasonal harvesting effort.

For simplicity, we first nondimensionalize system (1.1) with the following scaling:

$$\bar{t} = rt, \quad \bar{x} = \frac{x}{K}, \quad \bar{y} = \frac{\alpha y}{r}.$$

Dropping the bars, model (1.1) becomes

$$\begin{aligned} \dot{x} &= x(1 - x) - xye^{-bx} - (h + \gamma \sin(\tfrac{2\pi}{r} t)), \\ \dot{y} &= y(uxe^{-bx} - d), \end{aligned} \tag{1.2}$$

where $b = K\beta, u = \frac{\mu \alpha K}{r}, d = \frac{D}{r}, h = \frac{h_0}{Kr}, \gamma = \frac{\gamma_1}{Kr}$, and $h \geq \gamma$.

Now we describe the approaches that we use to study system (1.2). First, we consider system (1.2) with only constant-yield prey harvesting (that is, $\gamma = 0$) and show that several kinds of bifurcation phenomena, including saddle-node bifurcation, degenerate Hopf bifurcation, and Bogdanov–Takens bifurcation (i.e., cusp bifurcation of codimension 2), occur as the model parameters vary. The existence of two limit cycles and a homoclinic loop is also given, which reveals far richer dynamics compared to the case with no harvesting.

Next, from the dynamical systems point of view, we study the possible bifurcations in system (1.2) under the periodic perturbation $\gamma \sin(\frac{2\pi}{r}t)$. In studying the nature of turbulence in fluid mechanics, Landau [24] and Hopf [21] noticed that when a stable periodic solution becomes unstable, it is transferred into a stable quasi-periodic flow with two fundamental periods which can be represented on a two-dimensional torus. Mathematical studies of bifurcations of periodic solutions into invariant tori in finite dimensional dynamical systems have been given by Ruelle and Takens [34] (see also Lanford [25]) and Sell [35]. Bifurcations of homoclinic loops have been studied in Chow and Hale [10].

In studying the nonlinear dynamics of system (1.2) with seasonal prey harvesting, we will give sufficient conditions on the existence of an asymptotically stable periodic solution and the bifurcation of a stable periodic orbit into an invariant torus. The existence of bifurcation of a stable homoclinic loop into an invariant homoclinic torus is shown numerically. It is also shown that the initial species densities are very important for the persistence of the interacting species in terms of quasi-periodic solutions when the prey species is subjected to periodic harvesting. Our results show that the conclusions of Brauer and Sánchez [6], that in autonomous single population models the behaviors of the model with periodic harvesting are analogous to those of the model with no harvesting (but with an asymptotically stable periodic solution instead of an asymptotically stable equilibrium), still hold for the interacting species models as long as the initial species densities are chosen suitably. Moreover, our numerical simulations show that a stable limit cycle or a stable homoclinic loop in the model will be transformed into an invariant torus or an invariant homoclinic torus, respectively, by seasonal prey harvesting. To the best of our knowledge, such bifurcations have not been observed in predator-prey systems in any literature.

The paper is organized as follows. In section 2, we study the existence of various types of equilibria in model (1.2) with constant-yield harvesting. We also describe the phase portraits and the biological ramifications of our results. In section 3, we discuss possible bifurcations of the model (1.2) with constant-yield harvesting depending on all parameters and show that the model exhibits saddle-node bifurcation, degenerate Hopf bifurcation, and Bogdanov–Takens bifurcation in terms of the original model parameters. In section 4, the existence of an asymptotically stable periodic solution in system (1.2) and bifurcation of a stable periodic orbit into an invariant torus are established, and numerical simulations on the bifurcations of an invariant torus and an invariant homoclinic torus are also given. The paper ends with a brief discussion in section 5.

2. Constant-yield harvesting: Stability.

First of all, we carry out a qualitative analysis of model (1.2) with constant-yield harvesting, that is, $\gamma = 0$. To do that we rewrite (1.2) as

$$\begin{aligned} \dot{x} &= x(1-x) - xye^{-bx} - h \triangleq f_1(x,y), \\ \dot{y} &= y(uxe^{-bx} - d) \triangleq f_2(x,y), \end{aligned} \tag{2.1}$$

where b, h, d, and u are positive parameters. From the biological point of view, we study the dynamics of system (2.1) in the closed first quadrant R_+^2. Thus, we consider only the biologically meaningful initial conditions

$$x(0) \geq 0, \quad y(0) \geq 0.$$

We can show that the solution of (2.1) with nonnegative initial conditions exists and is unique. Notice that the x-axis is invariant under the flow. However, the y-axis is not. Any solution touching the y-axis crosses out of the first quadrant. Thus, the first quadrant is not positively invariant under the flow generated by system (2.1).

2.1. Equilibria. We can see that system (2.1) has six possible equilibria:

$$\begin{aligned} &A = (x_1, 0),\ B = (x_2, 0),\ C = (x_3, y_3), \\ &D = (x_4, y_4),\ E = \left(\frac{1}{2}, 0\right),\ F = \left(\frac{1}{b}, e - hbe - \frac{e}{b}\right), \end{aligned}$$

where

$$\begin{aligned} x_1 &= \frac{1 - \sqrt{1-4h}}{2}, \quad x_2 = \frac{1 + \sqrt{1-4h}}{2}, \\ u x_3 e^{-b x_3} - d &= 0, \quad u x_4 e^{-b x_4} - d = 0, \\ y_3 &= \frac{(x_3 - x_3^2 - h)(e^{b x_3})}{x_3}, \quad y_4 = \frac{(x_4 - x_4^2 - h)(e^{b x_4})}{x_4}, \\ h_1 &= x_3 - x_3^2, \quad h_2 = x_4 - x_4^2. \end{aligned}$$

THEOREM 2.1. *The existence of equilibria of system* (2.1), *according to the values of parameters, is summarized in Table* 1.

TABLE 1
Equilibria of system (2.1).

Cases	Equilibria
$h > \frac{1}{4}$	none
$h = \frac{1}{4}$	E
$0 < h < \frac{1}{4}$ and $u < bed$	A and B
$\frac{b-1}{b^2} \leq h < \frac{1}{4}$ and $u = ebd$	A and B
$\max\{h_1, h_2\} < h < \frac{1}{4}$ and $u > bed$	A and B
$0 < h < \frac{b-1}{b^2}$ and $u = bed$	A, B and F
$h_2 < h < h_1$ and $u > bed$	A, B and C
$h_1 < h < h_2$ and $u > bed$	A, B and D
$0 < h < \min\{h_1, h_2\}$ and $u > bed$	A, B, C and D

Proof. Consider an equilibrium of system (2.1) with coordinates (x_0, y_0), where x_0, y_0 are nonnegative solutions of the algebraic equations

$$\begin{aligned} &x(1-x) - xye^{-bx} - h = 0, \\ &y(uxe^{-bx} - d) = 0. \end{aligned} \tag{2.2}$$

By the second equation of (2.2), we have $y = 0$ or $uxe^{-bx} - d = 0$.

(1) If $y = 0$, the first equation of (2.2) yields

$$x^2 - x + h = 0, \tag{2.3}$$

whose discriminant is $\Delta := 1 - 4h$. It follows that (i) when $h > \frac{1}{4}$, (2.3) has no real roots; (ii) when $h = \frac{1}{4}$, (2.3) has only one positive real root $\frac{1}{2}$; and (iii) when $0 < h < \frac{1}{4}$, (2.3) has two positive real roots x_1 and x_2, which correspond to the boundary equilibria A, B of system (2.1).

(2) If

$$uxe^{-bx} - d = 0, \tag{2.4}$$

we let $p(x) = uxe^{-bx}$; then $p(x)$ attains its maximum $\frac{u}{be}$ at $\frac{1}{b}$ (see Figure 2.1), and (i) when $u < bed$, (2.4) does not have any real root; (ii) when $u = bed$, the only positive real root of (2.4) is $x = \frac{1}{b}$, which corresponds to the equilibrium $F = (\frac{1}{b}, e - hbe - \frac{e}{b})$ of (2.2). Note that $e - hbe - \frac{e}{b} < 0$ if $\frac{b-1}{b^2} < h < \frac{1}{4}$; $e - hbe - \frac{e}{b} = 0$ if $h = \frac{b-1}{b^2}$ and F becomes A or B; $e - hbe - \frac{e}{b} > 0$ if $0 < h < \frac{b-1}{b^2}$ and F lies in the interior of R_+^2; and (iii) when $u > bed$, (2.4) has two positive real roots x_3 and x_4 which correspond to the equilibria $C = (x_3, y_3)$ and $D = (x_4, y_4)$ of (2.2). Thus system (2.1) has three equilibria A, B, C if $h_2 < h < h_1$; three equilibria A, B, D if $h_1 < h < h_2$; and four equilibria A, B, C, D if $0 < h < \max\{h_1, h_2\}$. $\square$

Theorem 2.1 implies that when $h > \frac{1}{4}$, system (2.1) has no equilibria, and $\frac{dx}{dt} < 0$ in R_+^2. The dynamics of system (2.1) are trivial in R_+^2; every trajectory in R_+^2 will cross the y-axis and go out of R_+^2 in finite time (see also Figure 2.2(a)). This indicates that the prey species becomes extinct, which in turn drives predators to extinction. That is, overharvesting occurs. When $0 < h \leq \frac{1}{4}$, there exist some initial values such that the prey population in system (2.1) persists. Thus, $h_{MSY} = \frac{1}{4}$ for system (2.1) from Theorem 2.1. Hence, the constant-yield harvesting rate h must satisfy $0 < h < \frac{1}{4}$. In the following, we will study the nonlinear dynamics of system (2.1) when $0 < h < \frac{1}{4}$.

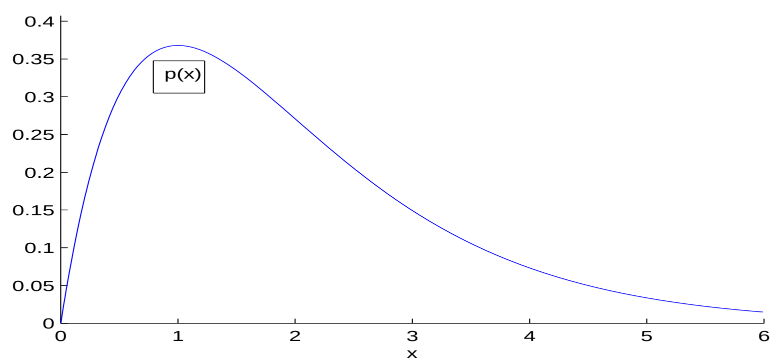

FIG. 2.1. *The graph of* $p(x) = uxe^{-bx}$.

2.2. Types and stability of equilibria. Now we determine the types and stability of the equilibria obtained in the last subsection. The Jacobian matrix takes the form

$$Df(x,y) = \begin{pmatrix} 1-2x-e^{-bx}y+bxye^{-bx} & -xe^{-bx} \\ yue^{-bx}-ubxye^{-bx} & -d+uxe^{-bx} \end{pmatrix}, \tag{2.5}$$

where $f=(f_1,f_2)^T$, and x and y are coordinates of these equilibria.

We first consider equilibria A, B, C, and D and will consider E, F later.

THEOREM 2.2. *The types of equilibria A, B, C, and D, according to the values of parameters, are given in Table* 2. *Without loss of generality, we assume that $x_3 < x_4$. The phase portraits of system* (2.1) *without any equilibrium or with two boundary equilibria are shown in Figure* 2.2.

TABLE 2
Types of equilibria of system (2.1).

Cases	Equilibria	Type
$\max\{0, \frac{b-1}{b^2}\} < h < \frac{1}{4}$ and $u \le bed$	A and B	A is a hyperbolic saddle, B is a hyperbolic stable node
$h = \frac{b-1}{b^2}$, $b > 2$, and $u = bed$	A and B	A is a nonhyperbolic saddle, B is a hyperbolic stable node
$h = \frac{b-1}{b^2}$, $0 < b < 2$, and $u = bed$	A and B	A is a hyperbolic saddle, B is a nonhyperbolic stable node
$\max\{h_1, h_2\} < h < \frac{1}{4}$, $u > bed$, and $x_3 < \frac{1}{2} < x_4$	A and B	A is a hyperbolic unstable node, B is a hyperbolic saddle
$\max\{h_1, h_2\} < h < \frac{1}{4}$, $u > bed$, and $x_3 > \frac{1}{2}$ (or $x_4 < \frac{1}{2}$)	A and B	A is a hyperbolic saddle, B is a hyperbolic stable node
$h_2 < h < h_1$ and $u > bed$	A, B, and C	A and B are hyperbolic saddles, C is an antisaddle
$h_1 < h < h_2$ and $u > bed$	A, B, and D	A is a hyperbolic unstable node, B is a hyperbolic stable node, D is a hyperbolic saddle
$0 < h < \min\{h_1, h_2\}$ and $u > bed$	A, B, C, and D	A and D are hyperbolic saddles, B is a hyperbolic stable node, C is an antisaddle

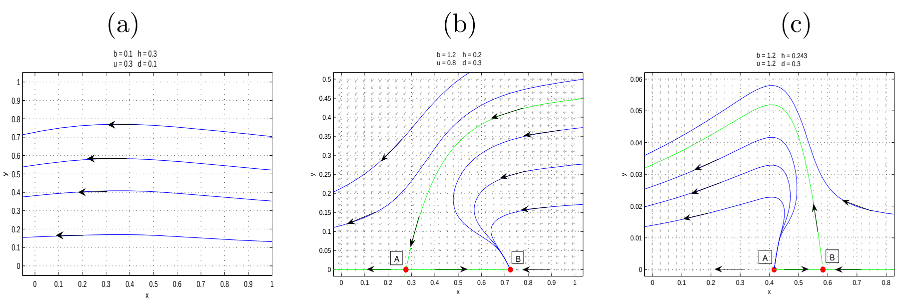

FIG. 2.2. *The phase portraits of system* (2.1) *without any equilibrium or with two boundary equilibria.* (a) *No equilibrium.* (b)–(c) *Two boundary equilibria.*

Proof. We first consider $A=(x_1,0)$ and $B=(x_2,0)$, where $x_1 = \frac{1-\sqrt{1-4h}}{2}, x_2 = \frac{1+\sqrt{1-4h}}{2}$, $0 < h < \frac{1}{4}$. By (2.5), we have

$$Df(A) = \begin{pmatrix} 1-2x_1 & -x_1e^{-bx_1} \\ 0 & -d+ux_1e^{-bx_1} \end{pmatrix}, \; Df(B) = \begin{pmatrix} 1-2x_2 & -x_2e^{-bx_2} \\ 0 & -d+ux_2e^{-bx_2} \end{pmatrix}.$$

It follows that $1-2x_i$ and $-d+ux_ie^{-bx_i}(i=1,2)$ are the eigenvalues of $Df(A)$ and $Df(B)$. Moreover, we can see that $1-2x_1=\sqrt{1-4h}>0, 1-2x_2=-\sqrt{1-4h}<0$, and have the following results:

Case 1. $ux_ie^{-bx_i}-d<0$ if $u<bed$.

Case 2. $ux_ie^{-bx_i}-d<0$ and $x_i\neq\frac{1}{b}$ if $u=bed$ and $\max\{0,\frac{b-1}{b^2}\}<h<\frac{1}{4}$.

Case 3. $ux_1e^{-bx_1}-d=0, ux_2e^{-bx_2}-d<0$ if $u=bed$, $h=\frac{b-1}{b^2}$, and $b>2$.

Case 4. $ux_1e^{-bx_1}-d<0, ux_2e^{-bx_2}-d=0$ if $u=bed$, $h=\frac{b-1}{b^2}$, and $0<b<2$.

Case 5. $ux_ie^{-bx_i}-d>0$ if $u>bed$, $\max\{h_1,h_2\}<h<\frac{1}{4}$, and $x_3<\frac{1}{2}<x_4$.

Case 6. $ux_ie^{-bx_i}-d<0$ if $u>bed$, $\max\{h_1,h_2\}<h<\frac{1}{4}$, and $x_3>\frac{1}{2}$ (or $x_4<\frac{1}{2}$).

Case 7. $ux_1e^{-bx_1}-d<0$ and $ux_2e^{-bx_2}-d>0$ if $u>bed$ and $h_2<h<h_1$.

Case 8. $ux_1e^{-bx_1}-d>0$ and $ux_2e^{-bx_2}-d<0$ if $u>bed$ and $h_1<h<h_2$.

Case 9. $ux_ie^{-bx_i}-d<0$ if $u>bed$ and $0<h<\min\{h_1,h_2\}$.

The types of A and B are obvious except in Cases 3 and 4, in which $A=(\frac{1}{b},0)(b>2)$ and $B=(\frac{1}{b},0)(0<b<2)$ are nonhyperbolic. Now we consider A and B when they are nonhyperbolic.

Translate $A=(\frac{1}{b},0)$ into the origin and expand system (2.1) in a power series around the origin. Let $X=x-\frac{1}{b}, Y=y$. Then system (2.1) can be rewritten as

$$\begin{aligned}\dot{X}&=(1-\tfrac{2}{b})X-\tfrac{1}{be}Y-X^2+\tfrac{b}{2e}X^2Y+P_1(X,Y),\\ \dot{Y}&=-\tfrac{ub}{2e}X^2Y+Q_1(X,Y),\end{aligned}\tag{2.6}$$

where $P_1(X,Y)$ and $Q_1(X,Y)$ are C^∞ functions of order at least four in (X,Y).

Make an affine transformation,

$$X=-\frac{1}{be}x+y, Y=\left(\frac{2}{b}-1\right)x;$$

system (2.6) becomes

$$\begin{aligned}\dot{x}&=-\tfrac{u}{2be^3}x^3-\tfrac{bu}{2e}xy^2+\tfrac{u}{e^2}x^2y+P_2(x,y),\\ \dot{y}&=(\tfrac{b-2}{b})y-\tfrac{1}{b^2e^2}x^2+\tfrac{2}{be}xy-y^2+Q_2(x,y),\end{aligned}\tag{2.7}$$

where $P_2(x,y)$ and $Q_2(x,y)$ are C^∞ functions of order at least four and three in (x,y), respectively.

Let $\tau=(\frac{b-2}{b})t$; then system (2.7) can be rewritten as

$$\begin{aligned}\dot{x}&=-\tfrac{u}{2e^3(b-2)}x^3-\tfrac{b^2u}{2e(b-2)}xy^2+\tfrac{bu}{(b-2)e^2}x^2y+P_3(x,y),\\ \dot{y}&=y-\tfrac{1}{e^2b(b-2)}x^2+\tfrac{2}{e(b-2)}xy-\tfrac{b}{b-2}y^2+Q_3(x,y),\end{aligned}\tag{2.8}$$

where $P_3(x,y)$ and $Q_3(x,y)$ are C^∞ functions of order at least four and three in (x,y), respectively. Since the coefficient of x^3 in the first equation of (2.8) is $-\frac{u}{e^3(b-2)}\neq 0$ (<0 if $b>2$; >0 if $0<b<2$), by Theorem 7.1 in Zhang et al. [41] and $\tau=(\frac{b-2}{b})t$, we know that $A=(\frac{1}{b},0)$ is a nonhyperbolic saddle if $b>2$; $B=(\frac{1}{b},0)$ is a nonhyperbolic stable node as $t:0\mapsto+\infty$ if $0<b<2$.

We then consider $C=(x_3,y_3)$ and $D=(x_4,y_4)$. By (2.5), we have

$$\mathrm{Det}(Df(C))=ue^{-bx_3}(1-bx_3)(-x_3^2+x_3-h),\ \ \mathrm{Det}(Df(D))=ue^{-bx_4}(1-bx_4)(-x_4^2+x_4-h).$$

Since $x_3<\frac{1}{b}<x_4$ and $x_i-x_i^2-h>0$ $(i=3,4)$, it follows that $\mathrm{Det}(Df(C))>0$ and $\mathrm{Det}(Df(D))<0$. So, D is a hyperbolic saddle and C is an antisaddle. □

THEOREM 2.3. *When $h=\frac{1}{4}$, system* (2.1) *has a unique singular point $E=(\frac{1}{2},0)$.*

(i) *It is a saddle-node if* $u \neq 2de^{\frac{b}{2}}$, *and it is attracting (repelling) if* $u < 2de^{\frac{b}{2}}$ $(u > 2de^{\frac{b}{2}})$.

(ii) *It is a degenerate saddle if* $u = 2de^{\frac{b}{2}}$ *and* $0 < b < 2$.

(iii) *It is a saddle-node if* $u = 2de^{\frac{b}{2}}$ *and* $b = 2$ *(that is,* $u = 2ed$*).*

(iv) *It is a degenerate singular point, and* $S_\delta((\frac{1}{2}, 0))$ *consists of one hyperbolic sector and one elliptic sector if* $u = 2de^{\frac{b}{2}}$ *and* $b > 2$, *where* $S_\delta((\frac{1}{2}, 0))$ *is the neighborhood of* $(\frac{1}{2}, 0)$ *with sufficient small radius* δ.

The phase portraits are shown in Figure 2.3.

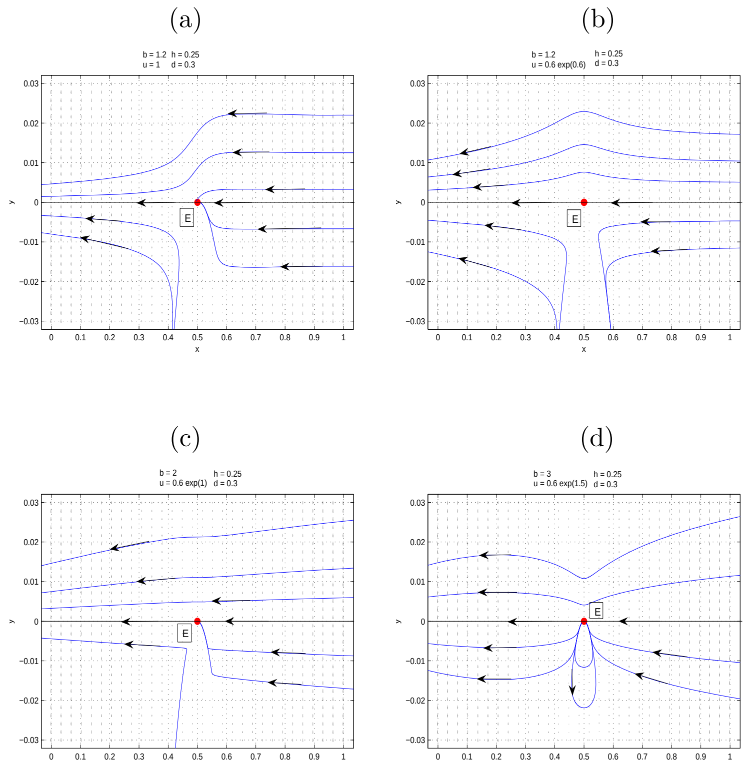

FIG. 2.3. *The phase portraits of system* (2.1) *with only one boundary equilibrium when* $h = \frac{1}{4}$. (a) $u \neq 2de^{\frac{b}{2}}$; (b) $u = 2de^{\frac{b}{2}}$ *and* $0 < b < 2$; (c) $u = 2de^{\frac{b}{2}}$ *and* $b = 2$; (d) $u = 2de^{\frac{b}{2}}$ *and* $b > 2$.

Proof. By (2.5), we have

$$Df(E) = \begin{pmatrix} 0 & -\frac{1}{2}e^{-\frac{b}{2}} \\ 0 & \frac{u}{2}e^{-\frac{b}{2}} - d \end{pmatrix}.$$

The eigenvalues of $Df(E)$ are $\lambda_1 = 0$ and $\lambda_2 = \frac{u}{2}e^{-\frac{b}{2}} - d$.

The transformation $(X, Y) = (x - \frac{1}{2}, y)$ translates the equilibrium E to the origin. In a neighborhood of the origin, system (2.1) becomes

$$\begin{aligned} \dot{X} &= -\tfrac{1}{2}e^{-\frac{b}{2}}Y - X^2 - (1 - \tfrac{b}{2})e^{-\frac{b}{2}}XY - b(\tfrac{b}{4} - 1)e^{-\frac{b}{2}}X^2Y + P_1(X, Y), \\ \dot{Y} &= (\tfrac{u}{2}e^{-\frac{b}{2}} - d)Y + u(1 - \tfrac{b}{2})e^{-\frac{b}{2}}XY + ub(\tfrac{b}{4} - 1)e^{-\frac{b}{2}}X^2Y + Q_1(X, Y), \end{aligned} \tag{2.9}$$

where $P_1(X,Y)$ and $Q_1(X,Y)$ are C^∞ functions of order at least four in (X,Y).

If $\lambda_2 \neq 0$, let $X = x - \frac{1}{2}e^{-\frac{b}{2}}y, Y = (\frac{u}{2}e^{-\frac{b}{2}} - d)y$; then system (2.9) becomes

$$\begin{aligned}\dot{x} &= -x^2 + \alpha_1 xy + \alpha_2 y^2 + P_2(x,y),\\ \dot{y} &= \beta_1 y + \beta_2 xy + \beta_3 y^2 + Q_2(x,y),\end{aligned} \tag{2.10}$$

where $P_2(x,y)$ and $Q_2(x,y)$ are C^∞ functions in (x,y) of order at least three in (x,y), and

$$\alpha_1 = \frac{1}{2}e^{-\frac{b}{2}}(2 - d(b-2)), \quad \alpha_2 = \frac{1}{4}e^{-b}(-1 + d(b-2)),$$
$$\beta_1 = \frac{u}{2}e^{-\frac{b}{2}} - d, \quad \beta_2 = u\left(1 - \frac{b}{2}\right)e^{-\frac{b}{2}}, \quad \beta_3 = -\frac{1}{2}u\left(1 - \frac{b}{2}\right)e^{-b}.$$

Introducing a new time variable τ by $\tau = \beta_1 t$ and still denoting τ with t, we obtain

$$\begin{aligned}\dot{x} &= -\tfrac{1}{\beta_1}x^2 + \tfrac{\alpha_1}{\beta_1}xy + \tfrac{\alpha_1}{\beta_1}y^2 + P_3(x,y),\\ \dot{y} &= y + \tfrac{\beta_2}{\beta_1}xy + \tfrac{\beta_3}{\beta_1}y^2 + Q_3(x,y).\end{aligned} \tag{2.11}$$

Since the coefficient of x^2 in the first equation of system (2.11) is $\frac{-1}{\beta_1} = \frac{-1}{\lambda_2} \neq 0$, Theorem 7.1 in Zhang et al. [41] implies that the equilibrium $E = (\frac{1}{2}, 0)$ is a saddle-node, which is attracting (repelling) if $u < 2de^{\frac{b}{2}}$ $(u > 2de^{\frac{b}{2}})$.

If $\lambda_2 = 0$, let $\tau = -\frac{1}{2}e^{-\frac{b}{2}}t$; then (2.9) becomes

$$\begin{aligned}\dot{X} &= Y + P_4(X,Y),\\ \dot{Y} &= Q_4(X,Y),\end{aligned} \tag{2.12}$$

where $P_4(X,Y)$ and $Q_4(X,Y)$ are C^∞ functions of order at least two in (X,Y). Let $Y + P_4(X,Y) = 0$; we obtain an implicit function

$$Y = \phi(X) = -2e^{\frac{b}{2}}X^2 + 2(2-b)e^{\frac{b}{2}}X^3 + I_4(X),$$

where $I_4(X)$ is a C^∞ function of order at least four. Replacing Y with $\phi(X)$, we have

$$\psi(X) \triangleq Q_4(X,\phi(X)) = 2u(2-b)e^{\frac{b}{2}}X^3 - (b^2 - 4b + 8)ue^{\frac{b}{2}}X^4 + I_5(X),$$

$$\delta(X) \triangleq \frac{\partial P_4}{\partial X}(X,\phi(X)) + \frac{\partial Q_4}{\partial Y}(X,\phi(X)) = (u(b-2) + 4e^{\frac{b}{2}})X + I_2(X),$$

where $I_5(X)$ and $I_2(X)$ are C^∞ functions of order at least five and two, respectively.

Denote

$$a_1 \triangleq 2u(2-b)e^{\frac{b}{2}}, \quad a_2 \triangleq -(b^2 - 4b + 8)ue^{\frac{b}{2}}, \quad b_1 \triangleq u(b-2) + 4e^{\frac{b}{2}}.$$

By Theorems 7.2 and 7.3 in Zhang et al. [41], if $0 < b < 2$, then $a_1 > 0$ and $(\frac{1}{2}, 0)$ is a saddle; if $b = 2$, then $a_1 = 0, a_2 < 0$, $b_1 \neq 0$, and $(\frac{1}{2}, 0)$ is a saddle-node; if $b > 2$, then $a_1 < 0$, $b_1 \neq 0$, $b_1^2 + 8a_1 \geq 0$, and $S_\delta((\frac{1}{2}, 0))$ consists of one hyperbolic sector and one elliptic sector. ∎

THEOREM 2.4. *If $0 < h < \frac{b-1}{b^2}$, $u = bed$, and $b > 1$, then system* (2.1) *has three equilibria, A, B, and F, and no closed orbits in R_+^2. Moreover,*

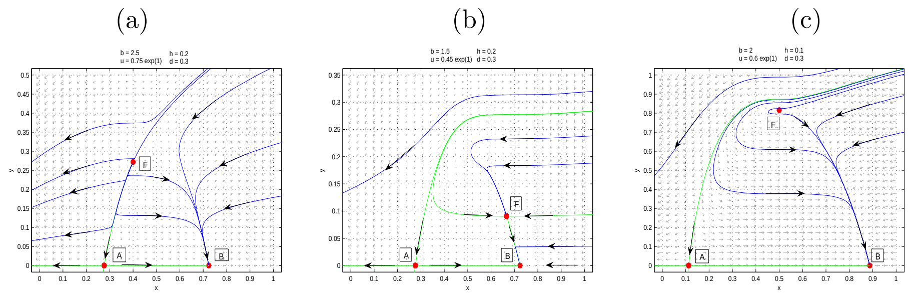

FIG. 2.4. *The phase portraits of system* (2.1) *when* $0 < h < \frac{b-1}{b^2}$*,* $u = bed$*, and* $b > 1$*.* (a) $b > 2$*;* (b) $b < 2$*;* (c) $b = 2$*.*

(i) *if* $b \neq 2$*, then* A, B*, and* F *are a hyperbolic saddle, a hyperbolic stable node, and a saddle-node, respectively, and* F *is attracting (repelling) if* $1 < b < 2$ *(*$b > 2$*);*

(ii) *if* $b = 2$*, then* A, B*, and* F *are a hyperbolic saddle, a hyperbolic stable node, and a cusp of codimension* 2*, respectively.*

The phase portraits are shown in Figure 2.4*.*

Proof. (1) The types of A and B can be obtained from Theorem 2.2 straightforwardly.

(2) If $b = 2$, F is a cusp of codimension 2. First, we translate $F(\frac{1}{2}, \frac{e}{2} - 2eh)$ to the origin and expand system (2.1) in a power series around the origin. Let $X = x - \frac{1}{2}$, $Y = y - \frac{e}{2} + 2eh$; then system (2.1) can be rewritten as

$$\begin{aligned} \dot{X} &= -\tfrac{1}{2e}Y - (\tfrac{1}{2} + 2h)X^2 + P_1(X, Y), \\ \dot{Y} &= (2uh - \tfrac{u}{2})X^2 + Q_1(X, Y), \end{aligned} \tag{2.13}$$

where $P_1(X, Y)$ and $Q_1(X, Y)$ are C^∞ functions of order at least three in (X, Y). Next, we make a time translation $\tau = -\frac{1}{2e}t$; then (2.13) can be rewritten as

$$\begin{aligned} \dot{X} &= Y + (e + 4eh)X^2 + P_2(X, Y), \\ \dot{Y} &= (eu - 4ehu)X^2 + Q_2(X, Y), \end{aligned} \tag{2.14}$$

where $P_2(X, Y)$ and $Q_2(X, Y)$ are C^∞ functions of order at least three in (X, Y). We take $x = X, y = Y + (e + 4eh)X^2 + P_2(X, Y)$; then (2.14) becomes

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= eu(1 - 4h)x^2 + 2e(1 + 4h)xy + R(x, y), \end{aligned} \tag{2.15}$$

where $R(x, y)$ is a C^∞ function of order at least three in (x, y). Since $eu(1 - 4h) > 0$ and $2e(1 + 4h) > 0$ (because $0 < h < \frac{1}{4}$), it follows that $F(\frac{1}{2}, \frac{e}{2} - 2eh)$ is a cusp of codimension 2.

(3) If $b \neq 2$, F is a saddle-node. The transformation $(X, Y) = (x - \frac{1}{b}, y - e + heb + \frac{e}{b})$ translates the equilibrium E to the origin. In a neighborhood of the origin, system (2.1) becomes

$$\begin{aligned} \dot{X} &= a_{10}X + a_{01}Y + a_{20}X^2 + P_1(X, Y), \\ \dot{Y} &= b_{20}X^2 + Q_1(X, Y), \end{aligned} \tag{2.16}$$

where $P_1(X,Y)$ and $Q_1(X,Y)$ are C^∞ functions of order at least three in (X,Y), and

$$a_{10} = 1 - \frac{2}{b},\ a_{01} = \frac{-1}{eb},\ a_{20} = \frac{-3+b-hb^2}{2},\ b_{20} = \frac{u(hb^2-b+1)}{2}.$$

Let $X = a_{01}x + y$, $Y = -a_{10}x$; then (2.16) becomes

(2.17)
$$\begin{aligned}\dot{x} &= -\tfrac{b_{20}a_{01}^2}{a_{10}}x^2 - \tfrac{2b_{20}a_{01}}{a_{10}}xy - \tfrac{b_{20}}{a_{10}}y^2 + P_2(x,y),\\ \dot{y} &= a_{10}y + (a_{20} - \tfrac{a_{01}b_{20}}{a_{10}})a_{01}^2x^2 + 2(a_{20} - \tfrac{a_{01}b_{20}}{a_{10}})a_{01}xy + (a_{20} - \tfrac{a_{01}b_{20}}{a_{10}})y^2 + Q_2(x,y),\end{aligned}$$

where $P_2(x,y)$ and $Q_2(x,y)$ are C^∞ functions of order at least three in (x,y).

Defining a new time variable τ by $\tau = a_{10}t$, and still denoting τ with t; we obtain

(2.18)
$$\begin{aligned}\dot{x} &= -\tfrac{b_{20}a_{01}^2}{a_{10}^2}x^2 - \tfrac{2b_{20}a_{01}}{a_{10}^2}xy - \tfrac{b_{20}}{a_{10}^2}y^2 + P_3(x,y),\\ \dot{y} &= y + (\tfrac{a_{20}}{a_{10}} - \tfrac{a_{01}b_{20}}{a_{10}^2})a_{01}^2x^2 + 2(\tfrac{a_{20}}{a_{10}} - \tfrac{a_{01}b_{20}}{a_{10}^2})a_{01}xy + (\tfrac{a_{20}}{a_{10}} - \tfrac{a_{01}b_{20}}{a_{10}^2})y^2 + Q_3(x,y),\end{aligned}$$

where $P_3(x,y)$ and $Q_3(x,y)$ are C^∞ functions at least of order three in (x,y). The coefficient of x^2 in the first equation of system (2.18) is $-\frac{b_{20}a_{01}^2}{a_{10}^2} > 0$ since $0 < h < \frac{b-1}{b^2}$; then the equilibrium F is a saddle-node, which is attracting (repelling) if $1 < b < 2$ ($b > 2$). Since the closed orbit must include the equilibria in its interior whose indices sum to one, system (2.1) does not have a closed orbit in R_+^2 under the conditions of Theorem 2.4. ▯

THEOREM 2.5. *If $u > bed$ and $0 < h < h_1$, then $C = (x_3, y_3)$ is a positive equilibrium of system* (2.1). *Let $h_3 = \frac{bx_3^3 - bx_3^2 + x_3^2}{1 - bx_3}$; then C is*
(i) *a hyperbolic stable focus (or node) if $h < h_3$;*
(ii) *a weak focus or center if $h = h_3$;*
(iii) *a hyperbolic unstable focus (or node) if $h > h_3$.*

Proof. From Theorem 2.2 we have $\mathrm{Det}(Df(C)) > 0$. On the other hand,

$$\begin{aligned}\mathrm{Tr}(Df(C)) &= 1 - 2x_3 - e^{-bx_3}y_3 + bx_3y_3e^{-bx_3} = \frac{1-bx_3}{x_3}\left[h - \frac{bx_3^3 - bx_3^2 + x_3^2}{1-bx_3}\right]\\ &= \frac{1-bx_3}{x_3}(h - h_3).\end{aligned}$$

Since we have assumed $x_3 < x_4$, it follows that $0 < x_3 < \frac{1}{b}$. Hence $\mathrm{Tr}(Df(C)) < 0$ if $0 < h < \min\{h_3, h_1\}$; $\mathrm{Tr}(Df(C)) = 0$ if $0 < h = h_3 < h_1$; $\mathrm{Tr}(Df(C)) > 0$ if $0 < h_3 < h < h_1$. ▯

3. Constant-yield harvesting: Bifurcations.

In this section, we investigate various possible bifurcations in system (2.1) with constant-yield harvesting.

3.1. Saddle-node bifurcations.

From Theorems 2.1–2.3, we know that

$$SN_1 = \left\{(h,u,b,d) : h = \frac{1}{4}, \frac{u}{2}e^{-\frac{b}{2}} - d \neq 0, u, b, d > 0\right\}$$

is a saddle-node bifurcation surface. When the parameters pass from one side of the surface to the other side, the number of equilibria of system (2.1) changes from zero to two, and the two equilibria are boundary equilibria; one is a hyperbolic saddle and the other is a node. This is the first saddle-node bifurcation surface of the model. The biological interpretation for the first saddle-node bifurcation is that when $h_{MSY} = \frac{1}{4}$, the prey species is driven to extinction, and the system collapses when $h > \frac{1}{4}$, but the prey species does not become extinct for some initial data when $0 < h < \frac{1}{4}$. On the other hand, Theorems 2.1, 2.2, and 2.4 imply

$$SN_2 = \left\{(h, u, b, d) : u = bed, 0 < h < \frac{b-1}{b^2}, b \neq 2, a, d, u > 0\right\}$$

is also a saddle-node bifurcation surface. The second saddle-node bifurcation yields two positive equilibria. This implies that there exists a critical constant-yield harvesting $h_0 = \frac{b-1}{b^2}$ such that the predator species either becomes extinct or goes out of R_+^2 in finite time when $h > h_0$, and both predators and prey coexist in the form of a positive equilibrium for certain choices of initial values when $u = bed$ and $0 < h < h_0$.

3.2. Degenerate Hopf bifurcation. To study the order of the Hopf bifurcation of system (2.1), we transform it into a generalized Liénard system with a weak focus at the origin. The following lemma is Theorem 5.1 in Lamontagne, Coutu, and Rousseau [23]l; we also refer the reader to Etoua and Rousseau [15] and Xiao and Zhu [40] for similar results.

LEMMA 3.1. *For a generalized Liénard system,*

$$\begin{aligned} \dot{x} &= -y, \\ \dot{y} &= g(x) + yf(x), \end{aligned} \tag{3.1}$$

where

$$g(x) = \sum_{i=1}^{+\infty} A_i x^i, \quad f(x) = \sum_{j=1}^{+\infty} B_j x^j.$$

When $A_1 > 0$, the first two Lyapunov coefficients take the form

$$L_1 = \frac{B_2A_1 - A_2B_1}{8A_1^{\frac{3}{2}}},\ L_2 = \frac{1}{16A_1^{\frac{5}{2}}}\left(\frac{5}{3}A_2A_3B_1 - \frac{5}{3}A_1A_2B_3 + B_4A_1^2 - A_1A_4B_1\right).$$

Theorem 2.5 indicates that the positive equilibrium $C = (x_3, y_3)$ of system (2.1) is a center-type nonhyperbolic equilibrium when $u > bed$ and $0 < h = h_3 < h_1$. Thus, system (2.1) may exhibit a Hopf bifurcation. Notice that

$$h = h_3 = \tfrac{bx_3^3 - bx_3^2 + x_3^2}{1 - bx_3} < h_1 = x_3 - x_3^2 \Longrightarrow x_3 < \tfrac{1}{2}, \tag{3.2}$$

$$0 < h = h_3 \Longrightarrow x_3 > \tfrac{b-1}{b}, \tag{3.3}$$

$$u > bed \Longrightarrow x_3 < \tfrac{1}{b}. \tag{3.4}$$

THEOREM 3.2. *If $u > bed$ and $0 < h = h_3 < h_1$, then the equilibrium $C = (x_3, y_3)$ is*

(i) *a stable weak focus of multiplicity 1 if $L_{11} < 0$;*
(ii) *an unstable weak focus of multiplicity 1 if $L_{11} > 0$;*

(iii) *an unstable weak focus of multiplicity* 2 *if* $L_{11} = 0$, *where*

$$L_{11} = 2 + 6b^2 x_3 + 4b^3(-1 + x_3)x_3^2 - 2b(1 + x_3) + b^4(x_3^3 - 2x_3^4).$$

Proof. Rescale the time by dividing system (2.1) by xe^{-bx}. Since $xe^{-bx} > 0$ for all $x > 0$, the orientation of trajectories and the number of periodic solutions will not change. Next translate C to the origin by letting $(X, Y) = (x - x_3, y - y_3)$; then system (2.1) becomes

$$\text{(3.5)} \qquad \begin{aligned} \dot{X} &= P(X) - Y, \\ \dot{Y} &= (Y + y_3)\left(u - \tfrac{de^{b(X+x_3)}}{X+x_3}\right), \end{aligned}$$

where

$$P(X) = (1 - X - x_3)e^{b(X+x_3)} - \frac{he^{b(X+x_3)}}{X + x_3} - y_3.$$

The generalized Liénard system can be obtained by letting $(x, y) = (X, Y - P(X))$:

$$\text{(3.6)} \qquad \begin{aligned} \dot{x} &= -y, \\ \dot{y} &= g(x) + yf(x), \end{aligned}$$

where

$$g(x) = (P(x) + y_3)\left(u - \frac{de^{b(x+x_3)}}{x + x_3}\right), \quad f(x) = P'(x) + u - \frac{de^{b(x+x_3)}}{x + x_3},$$

and $P'(x)$ is the derivative of $P(x)$ with respect to x.

Following Lemma 3.1 and setting $d = ux_3e^{-bx_3}, h = h_3 = \frac{bx_3^3 - bx_3^2 + x_3^2}{1 - bx_3}$, we obtain

$$A_1 = -\tfrac{ue^{bx_3}(-1+2x_3)}{x_3}, \quad A_2 = -\tfrac{ue^{bx_3}(-1+2x_3)(2-2bx_3+b^2x_3^2)}{2x_3^2(-1+bx_3)},$$

$$A_3 = \tfrac{ue^{bx_3}(-3+9x_3-6bx_3^2+3b^2x_3^2-3b^2x_3^3-b^3x_3^3+2b^3x_3^4)}{3x_3^3(-1+bx_3)},$$

$$A_4 = \tfrac{ue^{bx_3}(24-96x_3+24bx_3+72bx_3^2-72b^2x_3^2+36b^2x_3^3+52b^3x_3^3-68b^3x_3^4-13b^4x_3^4+26b^4x_3^5)}{24x_3^4(-1+bx_3)},$$

$$B_1 = \tfrac{-u(-1+bx_3)^2+e^{bx_3}(2+2b(-1+x_3)+b^2(x_3-2x_3^2))}{x_3(-1+bx_3)},$$

$$B_2 = -\tfrac{e^{bx_3}(-6+6b+6b^2(-1+x_3)x_3+2b^3(1-2x_3)x_3^2)+u(2-4bx_3+3b^2x_3^2-b^3x_3^3)}{2x_3^2(-1+bx_3)},$$

$$B_3 = -\tfrac{u(6-12bx_3+9b^2x_3^2-4b^3x_3^3+b^4x_3^4)+3e^{bx_3}(-8+8b+4b^2(-2+x_3)x_3-4b^3(-1+x_3)x_3^2+b^4x_3^3(-1+2x_3))}{6x_3^3(-1+bx_3)},$$

$$\begin{aligned} B_4 = {} & \tfrac{u(24-48bx_3+36b^2x_3^2-16b^3x_3^3+5b^4x_3^4-b^5x_3^5)}{24x_3^4(-1+bx_3)} \\ & -\tfrac{4e^{bx_3}(30-30b-15b^2(-2+x_3)x_3-5b^4(-1+x_3)x_3^3+5b^3x_3^2(-3+2x_3)+b^5x_3^4(-1+2x_3))}{24x_3^4(-1+bx_3)}. \end{aligned}$$

By the formula of the first Lyapunov coefficient in Lemma 3.1, we have

$$L_1 = \frac{e^{bx_3}(2+6b^2x_3+4b^3(-1+x_3)x_3^2-2b(1+3x_3)+b^4(x_3^3-2x_3^4))}{16x_3^2\sqrt{\frac{-e^{bx_3}u(-1+2x_3)(-1+bx_3)^4}{x_3}}}.$$

Conditions (3.2) and (3.4) imply that L_1 is well defined and the sign of L_1 is the same as

$$L_{11}(x_3,b) = 2+6b^2x_3+4b^3(-1+x_3)x_3^2-2b(1+3x_3)+b^4(x_3^3-2x_3^4). \tag{3.7}$$

Therefore, when $u > bed, h = h_3$, and $L_{11} < 0$, $C = (x_3, y_3)$ is a stable weak focus of multiplicity 1; when $u > bed, h = h_3$, and $L_{11} > 0$, C is an unstable weak focus of multiplicity 1; when $u > bed, h = h_3$, and $L_{11} = 0$, C is a weak focus of multiplicity at least 2.

Now, we show that the order of the weak focus (x_3, y_3) is 2 if $L_{11} = 0$ and $h = h_3$. Using the formulas of the second Lyapunov coefficients in Lemma 3.1 and using the condition $L_{11} = 0$, we have

$$L_2 = \frac{2ue^{2bx_3}}{1152x_3^5\left(\sqrt{\frac{ue^{bx_3}(1-2x_3)}{x_3}}\right)^3(-1+bx_3)^3(1-2x_3)^2}L_{22},$$

where

(3.8)
$$\begin{aligned} L_{22}(x_3,b) = &-4(-5+25x_3-42x_3^2+32x_3^3)+b^2x_3(36-175x_3+316x_3^2-324x_3^3+16x_3^4)\\ &+4b(-5+13x_3+16x_3^2-64x_3^3+80x_3^4)\\ &+b^3x_3^2(11-102x_3+302x_3^2-336x_3^3+168x_3^4). \end{aligned}$$

So the sign of L_2 is determined by L_{22} when $L_{11} = 0$ and $h = h_3$. From conditions (3.2)–(3.4) it follows that

$$0 < x_3 < \tfrac{1}{2}, \quad 0 < b < 2, \tag{3.9}$$

and $L_2 > 0$ if $L_{22} < 0$.

Next we prove that $L_{22}(x_3, b)$ and $L_{11}(x_3, b)$ have no common roots when (3.9) is satisfied.

First, we consider the resultant $R(x_3)$ between $L_{11}(x_3, b)$ and $L_{22}(x_3, b)$ with respect to b, and we obtain

$$\begin{aligned}R(x_3) = &-4x_3^7(2412580x_3^6 - 8210392x_3^5 + 11651965x_3^4 - 9156240x_3^3\\ &+ 4053360x_3^2 - 931296x_3 + 85944)(2x_3 - 1)^{11}.\end{aligned}$$

By applying Sturm's theorem, we know that $R(x_3)$ has only one real root in $(0, \frac{1}{2})$. Moreover, through isolating the real roots of $R(x_3)$ by using the function realroot with accuracy $\frac{1}{1000}$ in Maple, we can prove that the root is in the closed subinterval $[\frac{423}{1024}, \frac{53}{128}]$ contained in $(0, \frac{1}{2})$.

On the other hand, we obtain the resultant $R(b)$ between $L_{11}(x_3, b)$ and $L_{22}(x_3, b)$ with respect to x_3 as follows:

$$\begin{aligned}R(b) = &-256b^{12}(b-1)(3581b^6 - 110968b^5 + 1104930b^4 - 3650076b^3 + 8598853b^2\\ &- 11151636b + 2412580)(b^2 - 4b + 2)^3(b-2)^5.\end{aligned}$$

By applying Sturm's theorem once more, we know that $R(b)$ has three distinct real roots in $(0, 2)$. By using the function realroot with accuracy $\frac{1}{1000}$ in Maple to $R(b)$, we claim that in $(0, 2)$ the first root is 1, the second root is simple and is in the closed subinterval $[\frac{271}{1024}, \frac{17}{64}]$, and the third root, which is of multiplicity three, is in the closed interval $[\frac{599}{1024}, \frac{75}{128}]$, respectively.

By direct computation, we have

$$L_{11}(x_3, 1) = -x_3^2(4 - 5x_3 + 2x_3^2),$$

which has no real roots as $0 < x_3 < \frac{1}{2}$. Therefore, if the polynomials $L_{11}(x_3, b)$ and $L_{22}(x_3, b)$ have one common root $(\bar{x}_3, \bar{b}) \in (0, \frac{1}{2}) \times (0, 1)$, the point $(\bar{x}_3, \bar{b})$ must be in the following two domains:

$$D_1 := \left\{(x_3, b)\Big|\ \frac{423}{1024} \le x_3 \le \frac{53}{128}, \frac{271}{1024} \le b \le \frac{17}{64}\right\}$$

and

$$D_2 := \left\{(x, b)\Big|\ \frac{423}{1024} \le x_3 \le \frac{53}{128}, \frac{599}{1024} \le b \le \frac{75}{128}\right\}.$$

We claim that there exists no $(\bar{x}_3, \bar{b})$ in D_i, $i = 1, 2$, for $L_{ii}(x_3, b) = 0$. As a matter of fact, we could prove that for all $(x_3, b) \in D_i$, for $i = 1, 2$, there holds $L_{ii}(x_3, b) > 0$.

By calculating the first order partial derivatives of $L_{11}(x_3, b)$ with respect to x_3 and b, respectively, we have

$$\begin{aligned}\frac{\partial L_{11}(x_3, b)}{\partial x_3} &= 6b^2 - 8b^3x_3 + 12b^3x_3^2 - 6b + 3b^4x_3^2 - 8b^4x_3^3,\\ \frac{\partial L_{11}(x_3, b)}{\partial b} &= 12bx_3 - 12b^2x_3^2 + 12b^2x_3^3 - 2 - 6x_3 + 4b^3x_3^3 - 8b^3x_3^4.\end{aligned}$$

Eliminating the variable b by computing the resultant $RL(x_3)$ between $\frac{\partial L_{11}(x_3,b)}{\partial x_3}$ and $\frac{\partial L_{11}(x_3,b)}{\partial b}$, we obtain that

$$RL(x_3) = -16x_3^6(1 + 3x_3)(683x_3^3 - 489x_3^2 + 121x_3 - 11),$$

which has no real roots in $(\frac{423}{1024}, \frac{53}{128})$ by Sturm's theorem. It implies that the polynomial $L_{11}(x_3, b)$ has no critical points in the interior of D_i, $i = 1, 2$, such that $\frac{\partial L_{11}(x_3,b)}{\partial x_3} = \frac{\partial L_{11}(x_3,b)}{\partial b} = 0$. Hence, the extremal value of the polynomial $L_{11}(x_3, b)$ can only be achieved at the boundary of D_i for $i = 1, 2$.

By direct computation, we obtain the values of the function $L_{11}(x_3, b)$ at four vertices of the rectangular domain D_1 as follows:

$$\begin{aligned} L_{11}\Big(\frac{423}{1024}, \frac{271}{1024}\Big) &= \frac{592974930883382763998559}{604462909807314587353088}, \\ L_{11}\Big(\frac{423}{1024}, \frac{17}{64}\Big) &= \frac{9018825847810201823}{9223372036854775808}, \\ L_{11}\Big(\frac{53}{128}, \frac{271}{1024}\Big) &= \frac{144597600389350315855}{147573952589676412928}, \\ L_{11}\Big(\frac{53}{128}, \frac{17}{64}\Big) &= \frac{2199235675593423}{2251799813685248}. \end{aligned}$$

On one pair of opposite sides of D_1, we obtain

$$\begin{aligned} L_{11}\Big(\frac{423}{1024}, b\Big) &= 2 + \frac{1269}{512}b^2 - \frac{107536329}{268435456}b^3 - \frac{2293}{512}b + \frac{6736140063}{549755813888}b^4, \\ L_{11}\Big(\frac{53}{128}, b\Big) &= 2 + \frac{159}{64}b^2 - \frac{210675}{524288}b^3 - \frac{287}{64}b + \frac{1637647}{134217728}b^4. \end{aligned}$$

By applying Sturm's theorem, it can be checked that none vanish for $\frac{271}{1024} \le b \le \frac{17}{64}$. With the same techniques, we can assert that on the other pair of opposite sides of D_1,

$$L_{11}\Big(x_3, \frac{271}{1024}\Big) \neq 0, \quad L_{11}\Big(x_3, \frac{17}{64}\Big) \neq 0,$$

as $\frac{423}{1024} \le x_3 \le \frac{53}{128}$. Hence the above arguments imply that $L_{11}(x_3, b)$ is identically positive on the closed rectangle D_1. Similarly, we could assert that $L_{11}(x_3, b) > 0$ for all $(x_3, b) \in D_2$.

Summarizing the above results, based on the eliminating theory by resultant and the algorithm of real root isolation, it follows that the polynomials $L_{11}(x_3, b)$ and $L_{22}(x_3, b)$ have no common roots in the domain $[0, \frac{1}{2}] \times [0, 2]$.

Finally, it remains to show that L_2 is strictly positive when $h = h_3$ and $L_{11} = 0$. Since L_{11} and L_{22} do not vanish simultaneously, L_2 does not change sign when $L_{11} = 0$ (by the intermediate value theorem). Let $b = 0.661481$, $x_3 = \frac{418}{1000}, d = \frac{1}{5}$, and $u = \frac{de^{bx_3}}{x_3}$; then $L_{11} = 0$, and $L_2 \doteq 0.244321 > 0$. Hence, we complete the proof. ∎

By the theory of Hopf bifurcation [41], we obtain the following results.

THEOREM 3.3. *Suppose that $u > bed$ and $0 < h = h_3 < h_1$.*

(i) *If $L_{11} < 0$, then there is one stable limit cycle in (2.1) as h increases from h_3.*

(ii) *If $L_{11} > 0$, then there is one unstable limit cycle in (2.1) as h decreases from h_3.*

(iii) *If $L_{11} = 0$, then there are two limit cycles in (2.1) as h increases from h_3 and L_{11} decreases from 0, the inner is stable, and the outer is unstable.*

In Figure 3.1, by incorporating the above analysis and using numerical simulations, we present the supercritical and subcritical Hopf bifurcations of codimension 1.

In Figure 3.2, we show the degenerate Hopf bifurcation and the existence of two limit cycles, where the stable one is in the interior of the unstable one.

These results and numerical simulations demonstrate that for some initial values, both species coexist in the form of a positive equilibrium, and for some other initial values, both species coexist in the form of unstable or stable oscillatory solutions.

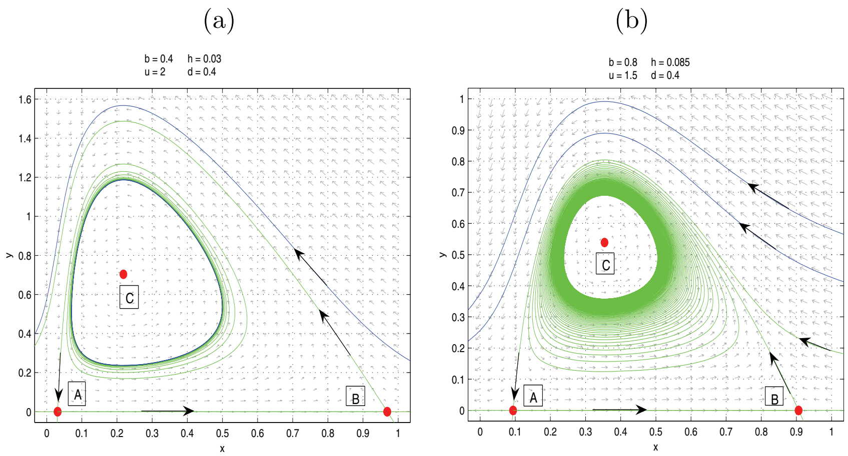

FIG. 3.1. (a) *An unstable limit cycle created by the subcritical Hopf bifurcation.* (b) *A stable limit cycle created by the supercritical Hopf bifurcation.*

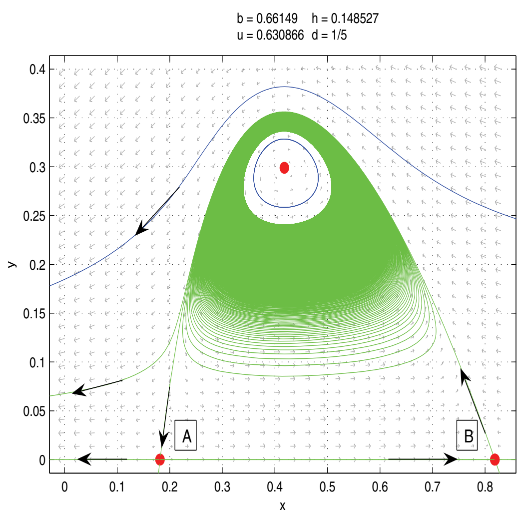

FIG. 3.2. *The existence of two limit cycles, where the inner is stable and the outer is unstable.*

3.3. Bogdanov–Takens bifurcation. Theorem 2.4 indicates that system (2.1) has a Bogdanov–Takens singularity $F = (\frac{1}{2}, \frac{1}{2}e - 2eh)$ when $b = 2, u = bed$, and $0 < h < \frac{b-1}{b^2}$. Let $b_0 = 2, u_0 = eb_0 d_0 = 2ed_0$, and $0 < h_0 < \frac{b_0-1}{b_0^2} = \frac{1}{4}$; we now show that system (2.1) undergoes Bogdanov–Takens bifurcation in a small neighborhood of $(\frac{1}{2}, \frac{1}{2}e - 2eh_0)$.

THEOREM 3.4. *If $b = 2, u = 2ed$, and $0 < h < \frac{1}{4}$, system* (2.1) *has a cusp $F = (\frac{1}{2}, \frac{1}{2}e - 2eh)$ of codimension* 2 *(i.e., Bogdanov–Takens singularity). If we choose b and d as bifurcation parameters, then system* (2.1) *undergoes Bogdanov–Takens bifurcation in a small neighborhood of F as (b, d) varies near $(2, \frac{\mu}{2e})$. Hence, there exist some parameter values such that system* (2.1) *has a stable limit cycle, and there exist some other parameter values such that system* (2.1) *has a stable homoclinic loop.*

Proof. Consider

$$\begin{aligned} \dot{x} &= x(1-x) - xye^{-(2+\lambda_1)x} - h_0, \\ \dot{y} &= y(2ed_0xe^{-(2+\lambda_1)x} - (d_0+\lambda_2)), \end{aligned} \tag{3.10}$$

where $0 < h_0 < \frac{1}{4}$ and $\lambda = (\lambda_1, \lambda_2)$ is a parameter vector in a small neighborhood of (0,0).

First, we translate the interior equilibrium F to the origin and expand system (3.10) in a power series around the origin. Let $X = x - \frac{1}{2}$ and $Y = y - \frac{1}{2}e + 2eh_0$. Then system (3.10) can be rewritten as

$$\begin{aligned} \dot{X} &= a_1 + a_2X + a_3Y + a_4X^2 + a_5XY + a_6X^3 + a_7X^2Y + P_1(X,Y,\lambda_1), \\ \dot{Y} &= b_1 + b_2X + b_3Y + b_4X^2 + b_5XY + Q_1(X,Y,\lambda_1), \end{aligned} \tag{3.11}$$

where $P_1(X,Y,\lambda_1)$ and $Q_1(X,Y,\lambda_1)$ are C^∞ functions of at least the fourth order and third order with respect to (X,Y), respectively, and

$$a_1 = \left(\frac{1}{4} - h_0\right)(1 - e^{-\lambda_1/2}), \quad a_2 = \left(\frac{1}{4} - h_0\right)\lambda_1 e^{-\lambda_1/2}, \quad a_3 = -\frac{1}{2}e^{-1-\frac{\lambda_1}{2}},$$

$$a_4 = -1 - \left(\frac{1}{8} - \frac{h_0}{2}\right)(-2+\lambda_1)(2+\lambda_1)e^{\frac{-\lambda_1}{2}}, \quad a_5 = \frac{1}{2}\lambda_1 e^{-1-\frac{\lambda_1}{2}},$$

$$a_6 = \left(\frac{1}{24} - \frac{h_0}{6}\right)(-4+\lambda_1)(2+\lambda_1)^2 e^{-\lambda_1/2}, \quad a_7 = -1 - \frac{1}{4}(-2+\lambda_1)(2+\lambda_1)e^{-1-\frac{\lambda_1}{2}},$$

$$b_1 = e(-d_0 + d_0e^{-\lambda_1/2} - \lambda_2)\left(\frac{1}{2} - 2h_0\right), \quad b_2 = -d_0\lambda_1\left(\frac{1}{2} - 2h_0\right)e^{1-\frac{\lambda_1}{2}},$$

$$b_3 = -d_0 - \lambda_2 + d_0e^{-\lambda_1/2}, \quad b_4 = \left(\frac{1}{4} - h_0\right)d_0(-4+\lambda_1^2)e^{1-\frac{\lambda_1}{2}}, \quad b_5 = -d_0\lambda_1 e^{-\lambda_1/2}.$$

Setting

$$\begin{aligned} x &= X, \\ y &= a_1 + a_2X + a_3Y + a_4X^2 + a_5XY + a_6X^3 + a_7X^2Y + P_1(X,Y,\lambda_1), \end{aligned}$$

we have

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= c_1 + c_2x + c_3y + c_4x^2 + c_5xy + c_6y^2 + R_1(x,y,\lambda_1,\lambda_2), \end{aligned} \tag{3.12}$$

where $R_1(x,y,\lambda_1,\lambda_2)$ is a C^∞ function of at least the third order with respect to (x,y), and

$$c_1 = a_3b_1 - a_1b_3, \quad c_2 = -\frac{-a_1^2a_5^2 + 2a_1^2a_3a_7 - a_3^2a_5b_1 - a_3^3b_2 + a_2a_3^2b_3 + a_1a_3^2b_5}{a_3^2},$$

$$c_3 = -\frac{-a_2a_3 + a_1a_5 - a_3b_3}{a_3},$$

$$c_4 = -\frac{a_1a_3a_4a_5 - a_1a_2a_5^2 - 3a_1a_3^2a_6 + 2a_1a_2a_3a_7 - a_3^2a_7b_1 - a_3^2a_5b_2 + a_3^2a_4b_3 - a_3^3b_4 + a_2a_3^2b_5}{a_3^2},$$

$$c_5 = -\frac{-2a_3^2a_4 + a_2a_3a_5 + a_1a_5^2 + a_1a_5^2 - 2a_1a_3a_7 - a_3^2b_5}{a_3^2}, \quad c_6 = \frac{a_5}{a_3}.$$

Once again introducing a new time variable τ by $dt = (1 - c_6x)d\tau$ and rewriting τ as t, we obtain

$$\begin{aligned} \dot{x} &= y(1 - c_6x), \\ \dot{y} &= (1 - c_6x)(c_1 + c_2x + c_3y + c_4x^2 + c_5xy + c_6y^2 + R_1(x, y, \lambda_1, \lambda_2)). \end{aligned} \tag{3.13}$$

Let $X = x, Y = y(1 - c_6x)$; we have

$$\begin{aligned} \dot{X} &= Y, \\ \dot{Y} &= d_1 + d_2X + d_3Y + d_4X^2 + d_5XY + R_2(X, Y, \lambda_1, \lambda_2), \end{aligned} \tag{3.14}$$

where $R_2(X, Y, \lambda_1, \lambda_2)$ is a C^∞ function of at least the third order with respect to (X, Y), and

$$d_1 = c_1, \quad d_2 = c_2 - 2c_1c_6, \quad d_3 = c_3, \quad d_4 = c_4 - 2c_2c_6 + c_1c_6^2, \quad d_5 = c_5 - c_3c_6.$$

Hence $d_4 > 0$ and $d_5 < 0$ when λ_i are small. Making the change of variables

$$x = X, \quad y = \frac{Y}{\sqrt{d_4}}, \quad \tau = \sqrt{d_4}t$$

and still denoting τ by t, we obtain

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= e_1 + e_2x + e_3y + x^2 + e_4xy + R_3(x, y, \lambda_1, \lambda_2), \end{aligned} \tag{3.15}$$

where

$$e_1 = \frac{d_1}{d_4}, \quad e_2 = \frac{d_2}{d_4}, \quad e_3 = \frac{d_3}{\sqrt{d_4}}, \quad e_4 = \frac{d_5}{\sqrt{d_4}}.$$

Letting $X = x + \frac{e_2}{2}, Y = y$, we rewrite (3.15) as

$$\begin{aligned} \dot{X} &= Y, \\ \dot{Y} &= \gamma_1 + \gamma_2Y + X^2 + \gamma_3XY + R_4(X, Y, \lambda_1, \lambda_2), \end{aligned} \tag{3.16}$$

where $R_4(X, Y, \lambda_1, \lambda_2)$ is a C^∞ function of at least the third order with respect to (X, Y), and

$$\gamma_1 = e_1 - \frac{e_2^2}{4}, \quad \gamma_2 = e_3 - \frac{e_2e_4}{2}, \quad \gamma_3 = e_4.$$

Since $\gamma_3 < 0$ when λ_i are small, setting

$$x = \gamma_3^2 X, \quad y = -\gamma_3^3 Y, \quad \tau = -\frac{t}{\gamma_3},$$

and still denoting τ by t, we finally have

$$\begin{aligned} \dot{x} &= y, \\ \dot{y} &= \xi_1 + \xi_2 y + x^2 - xy + R_5(x, y, \lambda_1, \lambda_2), \end{aligned} \tag{3.17}$$

where $R_5(x, y, \lambda_1, \lambda_2)$ is a C^∞ function of at least the third order with respect to (x, y), and

$$\xi_1 = \gamma_1 \gamma_3^4, \quad \xi_2 = -\gamma_2 \gamma_3.$$

Notice that we can express ξ_1 and ξ_2 in terms of λ_1 and λ_2 as

$$\begin{aligned} \xi_1 &= s_1\lambda_1 + s_2\lambda_2 + s_3\lambda_1^2 + s_4\lambda_1\lambda_2 + s_5\lambda_2^2 + o(|\lambda_1, \lambda_2|^2), \\ \xi_2 &= t_1\lambda_1 + t_2\lambda_2 + t_3\lambda_1^2 + t_4\lambda_1\lambda_2 + t_5\lambda_2^2 + o(|\lambda_1, \lambda_2|^2), \end{aligned} \tag{3.18}$$

where

$$s_1 = \frac{(1+4h_0)^4}{d_0^2(4h_0-1)^2}, \quad s_2 = \frac{2(1+4h_0)^4}{d_0^3(4h_0-1)^2}, \quad s_5 = -\frac{6(4h_0+1)^4(2-e+4eh_0)}{d_0^4(4h_0-1)^3},$$

$$s_3 = \frac{(1+4h_0)^3(8d_0^2(4h_0-1) - 3(4h_0-1)^2(4h_0+1) + d_0(-19+40h_0-48h_0^2+e(7-32h_0+16h_0^2)))}{2d_0^3(4h_0-1)^3},$$

$$s_4 = -\frac{(1+4h_0)^3(8d_0^2(1-4h_0) + 3(4h_0-1)^2(4h_0+1) + 2d_0(13-8+16h_0^2+e(-5+16h_0+16h_0^2)))}{d_0^4(4h_0-1)^3},$$

$$t_1 = \frac{(d_0-1)(4h_0+1)}{d_0(4h_0-1)}, \quad t_2 = \frac{2(4h_0+1)}{d_0(4h_0-1)}, \quad t_5 = -\frac{2(1+4h_0)(2-e+4eh_0)}{d_0^2(4h_0-1)^2},$$

$$\begin{aligned} t_3 = {} & \frac{1}{8d_0^2(4h_0-1)^2}(8d_0^3(4h_0-1) - (4h_0-1)^2(4h_0+1)(-7+e-12h_0+4eh_0) - 2d_0^2(5+48h_0^2+4e(4h_0-1)) \\ & +2d_0(17+12h_0-16h_0^2-192h_0^3+2e(-3+8h_0+16h_0^2))), \end{aligned}$$

$$t_4 = \frac{4d_0^2(4h_0-1) - 2d_0(8+e(-3+8h_0+16h_0^2)) + (4h_0+1)(6+24h_0-64h_0^2+e(-3+8h_0+16h_0^2))}{2d_0^2(4h_0-1)^2}.$$

Since

$$\left|\frac{\partial(\xi_1, \xi_2)}{\partial(\lambda_1, \lambda_2)}\right|_{\lambda=0} = \frac{2(1+4h_0)^5}{d_0^4(4h_0-1)^3} < 0$$

for $0 < h_0 < \frac{1}{4}$, the parameter transformation (3.18) is a homeomorphism in a small neighborhood of the origin, and ξ_1 and ξ_2 are independent parameters.

The results in Bogdanov [3, 4] and Takens [36] or Perko [29] now imply that system (3.17) undergoes Bogdanov–Takens bifurcation when λ is in a small neighborhood of the origin. The local representations of the bifurcation curves up to second-order approximations are defined as follows.

(1) The saddle-node bifurcation curve $SN = \{(\xi_1, \xi_2) : \xi_1 = 0, \xi_2 \neq 0\}$; i.e.,

$$\begin{aligned} SN = \Bigg\{ (\lambda_1, \lambda_2) : {} & \frac{(1+4h_0)^4}{d_0^2(4h_0-1)^2}\lambda_1 + \frac{2(1+4h_0)^4}{d_0^3(4h_0-1)^2}\lambda_2 - \frac{6(4h_0+1)^4(2-e+4eh_0)}{d_0^4(4h_0-1)^3}\lambda_2^2 \\ & - \frac{(1+4h_0)^3(8d_0^2(1-4h_0) + 3(4h_0-1)^2(4h_0+1) + 2d_0(13-8+16h_0^2+e(-5+16h_0+16h_0^2)))}{d_0^4(4h_0-1)^3}\lambda_1\lambda_2 \\ & + \frac{(1+4h_0)^3(8d_0^2(4h_0-1) - 3(4h_0-1)^2(4h_0+1) + d_0(-19+40h_0-48h_0^2+e(7-32h_0+16h_0^2)))}{2d_0^3(4h_0-1)^3}\lambda_1^2 = 0 \Bigg\}. \end{aligned}$$

(2) The Hopf bifurcation curve $H = \{(\xi_1, \xi_2) : \xi_2 = -\sqrt{-\xi_1}, \xi_1 < 0\}$; i.e.,

$$\begin{aligned}
H = \Bigg\{&(\lambda_1, \lambda_2) : \frac{(4h_0+1)^4}{d_0^2(4h_0-1)^2}\lambda_1 + \frac{2(4h_0+1)^4}{d_0^3(4h_0-1)^2}\lambda_2 + \frac{(4h_0+1)^2(4d_0^2(4h_0-1)+6(4h_0+1)^2(2-e+4eh_0))}{d_0^4(4h_0-1)^3}\lambda_2^2 \\
&-\frac{(4h_0+1)^2}{d_0^4(4h_0-1)^3}(4d_0^3(1-4h_0)+d_0^2(4+16h_0-128h_0^2)+3(1-16h_0^2)^2+2d_0(4h_0+1)(13-8h_0+16h_0^2 \\
&+e(-5+16h_0+16h_0^2)))\lambda_1\lambda_2 - \frac{(4h_0+1)^2}{2d_0^3(4h_0-1)^3}(2d_0^3(1-4h_0)+d_0^2(4+16h_0-128h_0^2)+3(16h_0^2-1)^2 \\
&+d_0(21+28h_0-112h_0^2+192h_0^3+e(-7+4h_0+112h_0^2-64h_0^3)))\lambda_1^2 = 0, \xi_1 < 0, \xi_2 < 0\Bigg\}.
\end{aligned}$$

(3) The homoclinic bifurcation curve $HL = \{(\xi_1, \xi_2) : \xi_2 = -\frac{5}{7}\sqrt{-\xi_1}, \xi_1 < 0\}$; i.e.,

$$\begin{aligned}
HL = \Bigg\{&(\lambda_1, \lambda_2) : \frac{25(4h_0+1)^4}{49d_0^2(4h_0-1)^2}\lambda_1 + \frac{50(4h_0+1)^4}{49d_0^3(4h_0-1)^2}\lambda_2 + \frac{196d_0^2(4h_0+1)^2(4h_0-1)-150(4h_0+1)^4(2+e(4h_0-1))}{49d_0^4(4h_0-1)^3}\lambda_2^2 \\
&-\frac{(4h_0+1)^2}{49d_0^4(4h_0-1)^3}(-196d_0^3(4h_0-1)+d_0^2(4+784h_0-3200h_0^2)+75(1-16h_0^2)^2+50d_0(4h_0+1)(13-8h_0+16h_0^2 \\
&+e(-5+16h_0+16h_0^2)))\lambda_1\lambda_2 - \frac{(4h_0+1)^2}{98d_0^3(4h_0-1)^3}(98d_0^3(1-4h_0)+d_0^2(4+784h_0-3200h_0^2)+75(1-16h_0^2)^2 \\
&+d_0(573+508h_0-2800h_0^2+4800h_0^3-25e(7-4h_0-112h_0^2+64h_0^3)))\lambda_1^2 = 0, \xi_1 < 0, \xi_2 < 0\Bigg\}. \qquad \square
\end{aligned}$$

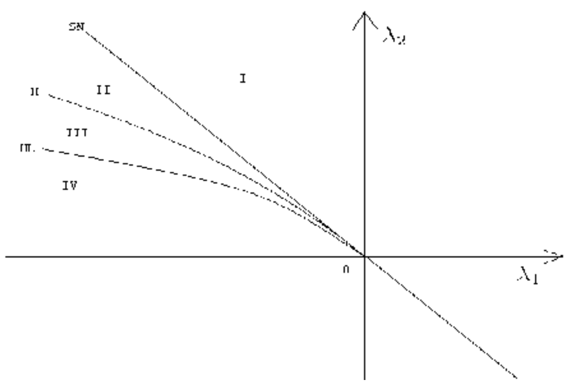

FIG. 3.3. *The bifurcation diagram of system* (3.10) *with* $h_0 = \frac{1}{8}, d_0 = 2$.

The bifurcation diagram and phase portraits of system (3.10) with $h_0 = \frac{1}{8}$ and $d_0 = 2$ are given in Figures 3.3 and 3.4, respectively. These bifurcation curves H, HL, and SN divide the small neighborhood of the origin in the (λ_1, λ_2) parameter plane into four regions (see Figure 3.3).

(a) When $(\lambda_1, \lambda_2) = (0, 0)$, the unique positive equilibrium is a cusp of codimension 2 (see Figure 3.4(a)).

(b) There are no positive equilibria when the parameters lie in region I (see Figure 3.4(b)). There exists one separatrix which converges to the boundary equilibrium A. The prey species goes extinct as the initial value density lies on the left of the separatrix, and the predators die out as the initial value density lies on the right of the separatrix.

(c) When the parameters lie on curve SN, there is a positive saddle-node equilibrium.

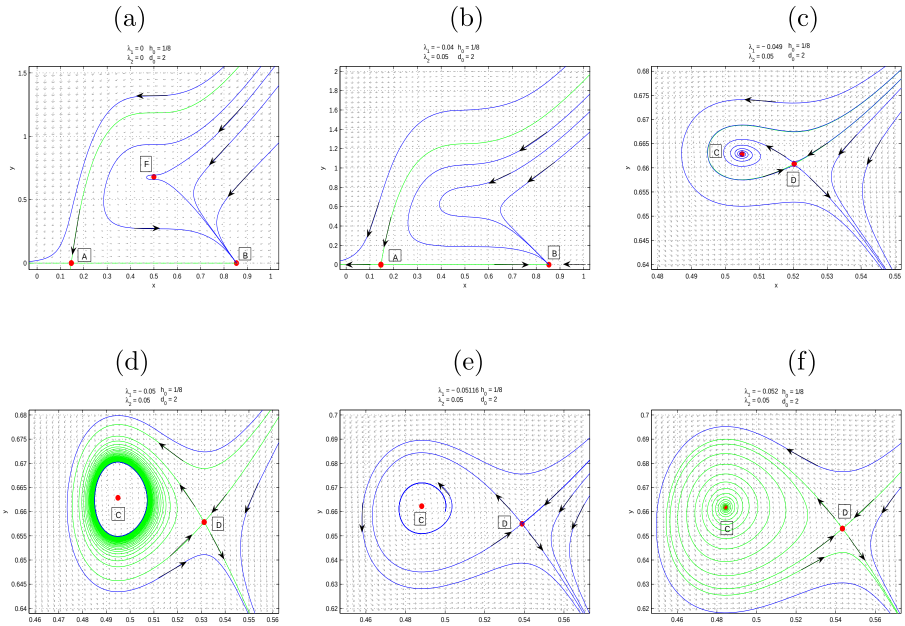

FIG. 3.4. *Phase portraits of system* (3.10) *with* $h_0 = \frac{1}{8}, d_0 = 2$*.* (a) *A cusp of codimension* 2 *when* $(\lambda_1, \lambda_2) = (0, 0)$*.* (b) *No positive equilibria when* $(\lambda_1, \lambda_2) = (-0.04, 0.05)$ *lies in region* I. (c) *A stable focus when* $(\lambda_1, \lambda_2) = (-0.049, 0.05)$ *lies in region* II. (d) *A stable limit cycle when* $(\lambda_1, \lambda_2) = (-0.05, 0.05)$ *lies in region* III. (e) *A stable homoclinic cycle when* $(\lambda_1, \lambda_2) = (-0.05116, 0.05)$ *lies on curve HL.* (f) *An unstable focus when* $(\lambda_1, \lambda_2) = (-0.052, 0.05)$ *lies in region* IV.

(d) Two positive equilibria, a stable focus and a saddle, appear through the saddle-node bifurcation when parameters cross SN into region II (see Figure 3.4(c)).

(e) A stable limit cycle appears through the supercritical Hopf bifurcation when the parameters cross H into region III (see Figure 3.4(d)), where the focus is unstable. The focus is a stable multiple one with multiplicity one when parameters lie on the curve H.

(f) A stable homoclinic cycle is generated through the homoclinic bifurcation when parameters pass region III and lie on curve HL (see Figure 3.4(e)).

(g) The relative locations of one stable manifold and one unstable manifold of the saddle $D(x_2, y_2)$ are reversed when parameters cross III into region IV (compare Figures 3.4(d) and 3.4(f)).

4. Seasonal harvesting: Periodic solutions and invariant tori. In this section we consider model (1.2) and assume that the prey population is harvested at a periodic rate. The harvesting reaches a maximum rate $h+\gamma$ at time $t = \frac{r}{4}+n$, where n is an integer (representing the year), and a minimum value $h-\gamma$ when $t = \frac{3r}{4}+n$, exactly half a year later [19].

We study the existence of an asymptotically stable periodic solution and the bifurcation of a stable periodic orbit into an invariant torus by theoretical analysis, and the bifurcation of a stable homoclinic loop into an invariant homoclinic torus by numerical simulations in system (1.2), respectively.

Rewrite system (1.2) as

$$\dot{Y} = f(Y) + \epsilon g(t, Y), \tag{4.1}$$

where $Y = (x, y)^T,\ f(Y) = (x(1-x) - xe^{-bx}y - h,\ y(uxe^{-bx} - d))^T,\ g(t, Y) = (-\sin(\frac{2\pi}{r}t), 0)^T$, and $\epsilon = \gamma$.

4.1. Existence of asymptotically stable periodic solutions. We need the following lemma which is Theorem 2 in Brauer [5].

LEMMA 4.1. *Let $f(Y)$ and $g(t, Y)$ be continuously differentiable with respect to the components of Y, and let $g(t, Y)$ be periodic in t with period w for each Y. Let Y_∞ be an equilibrium of system* (4.1) *when $\epsilon = 0$, which is asymptotically stable in the strong sense that the eigenvalues of the matrix $f_Y[Y_\infty]$ all have negative real parts. Then the perturbed system* (4.1) *has an asymptotically stable periodic solution $p(t, \epsilon)$ of the same period w for all sufficiently small ϵ with $\lim_{\epsilon \longrightarrow 0} p(t, \epsilon) = Y_\infty$.*

Applying Theorem 2.5 with the Lemma 4.1, we have the following theorem about the existence of an asymptotically stable periodic solution in system (1.2).

THEOREM 4.2. *If $u > bed$ and $0 < h < \min\{h_1, h_3\}$, then system* (4.1) *(i.e., system* (1.2)*) has an asymptotically stable periodic solution $p(t, \gamma)$ of period r for all sufficiently small γ with $\lim_{\gamma \longrightarrow 0} p(t, \gamma) = (x_3, y_3)$.*

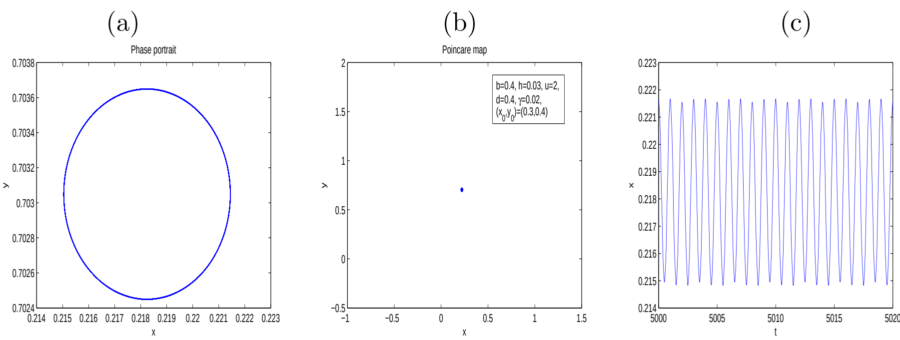

FIG. 4.1. (a) *The phase portrait of system* (1.2) *with* $r = 1, b = 0.4, h = 0.03, u = 2, d = 0.4, \gamma = 0.02$, *and initial value* $(x_0, y_0) = (0.3, 0.4)$. (b) *An attractor of the Poincaré map corresponding to* (a). (c) *The time series of the prey corresponding to* (a).

Figure 3.1(a) presents a hyperbolic stable focus C. The phase portrait and the corresponding attractor of the Poincaré map of system (1.2) in the (x, y)-plane are given in Figures 4.1(a) and 4.1(b), respectively, where $\gamma = 0.02, r = 1$, and the other parameter values are the same as those in Figure 3.1(a), that is, $b = 0.4, h = 0.03, u = 2$, and $d = 0.4$. We choose the initial density as $(x_0, y_0) = (0.3, 0.4)$, which is located in the attraction basin of the stable focus C of Figure 3.1(a). The attractor of the Poincaré map is a fixed point (see Figure 4.1(b)), which corresponds to a stable periodic orbit of system (1.2) (see Figure 4.1(a)). The time series of the prey population $x(t)$ corresponding to Figure 4.1(a) is given in Figure 4.1(c).

4.2. Bifurcation of stable periodic solutions into invariant tori. From Theorem 3.2 it follows that the interior equilibrium $C = (x_3, y_3)$ of system (2.1) is a stable weak focus of multiplicity one when $u > bed$, $0 < h = h_3 < h_1$, and $L_{11} < 0$, where the eigenvalues of $Df(x_3, y_3)$ are purely imaginary: $\pm\omega i$, $\omega = \sqrt{d(1 - 2x_3)}$, and $0 < x_3 < \frac{1}{2}$.

Combining Theorems 2.5 and 3.2 with the Theorem 6.3 in Chow and Hale [10], we have the following theorem about the existence of an asymptotically stable invariant torus in system (1.2).

THEOREM 4.3. *If $u > bed$, $0 < h - h_3 \ll 1$, and $L_{11} < 0$, then system* (2.1) *has a stable limit cycle enclosing $C = (x_3, y_3)$ by the supercritical Hopf bifurcation. If the nonresonant conditions*

$$r \neq 2k\pi, \quad k \in N^+, \tag{4.2}$$

$$m + n\frac{2\pi}{r} \neq 0, \quad 0 <\mid m \mid + \mid n \mid \leq 4, \quad m, n \in N, \tag{4.3}$$

are also satisfied, then system (1.2) *has an asymptotically stable invariant torus.*

Proof. We need to check the following three conditions in Theorem 6.3 in section 12 of Chow and Hale [10]:

$$\beta_0 \neq 0,$$
$$\det(e^{BT} - I) \neq 0,$$
$$m + n\frac{2\pi}{T} \neq 0, \quad 0 <\mid m \mid + \mid n \mid \leq 4, \quad m, n \in N,$$

where β_0 is the first Lyapunov constant for the center-type equilibrium $C = (x_3, y_3)$, and it is equivalent to L_{11} in system (2.1); T is the period of periodic perturbation, and $T = r$ in system (1.2); $B = \left(\begin{smallmatrix} 0 & 1 \\ -1 & 0 \end{smallmatrix}\right)$; and I is an identical matrix. Thus, these three conditions are satisfied under the nonresonant conditions (4.2) and (4.3). $\square$

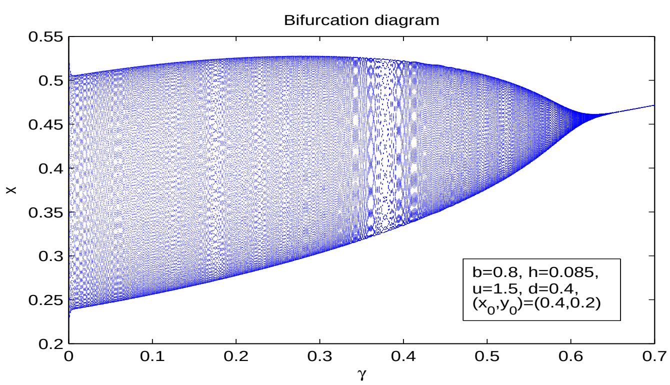

FIG. 4.2. *Bifurcation diagram of system* (1.2) *in terms of γ with $b = 0.8, h = 0.085, u = 1.5, d = 0.4, r = 1$, and initial value $(x_0, y_0) = (0.4, 0.2)$.*

In Figure 3.1(b), there exist an unstable focus C and a stable limit cycle enclosing C. The bifurcation diagram of system (1.2) with $r = 1$ in the (γ, x)-plane is given in Figure 4.2, where the other parameter values are the same as those in Figure 3.1(b), that is, $b = 0.8, h = 0.085, u = 1.5$, and $d = 0.4$. We choose the initial density as $(x_0, y_0) = (0.4, 0.2)$, which is located in the attraction basin of the stable limit cycle of Figure 3.1(b). The phase portrait, the attractor of the Poincaré map, and the time series for $\gamma = 0.08$ in Figure 4.2 are shown in Figures 4.3(a), (b), and (c), respectively, which show that the stable limit cycle in Figure 3.1(b) is bifurcated into an attracting invariant torus in Figure 4.2. This demonstrates that the solutions are

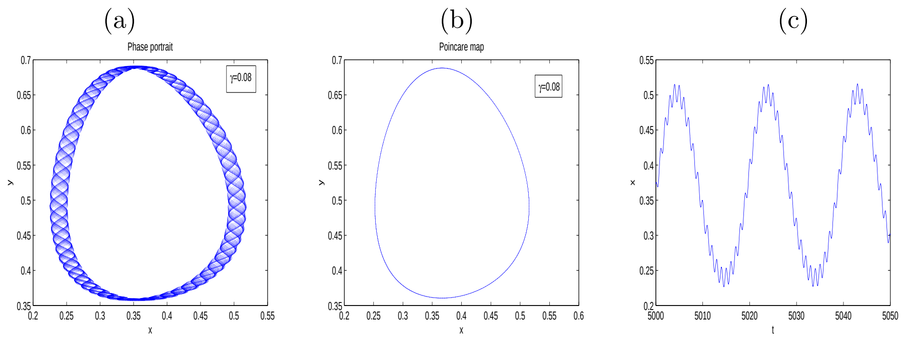

FIG. 4.3. (a) *Phase portrait for* $\gamma = 0.08$ *in Figure* 4.2. (b) *An attractor of the Poincaré map corresponding to* (a). (c) *The time series of the prey corresponding to* (a).

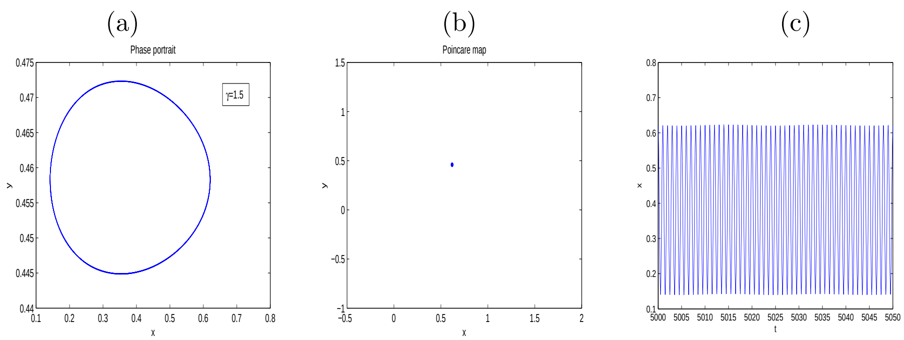

FIG. 4.4. (a) *Phase portrait for* $\gamma = 1.5$ *in Figure* 4.2. (b) *An attractor of the Poincaré map corresponding to* (a). (c) *The time series of the prey corresponding to* (a).

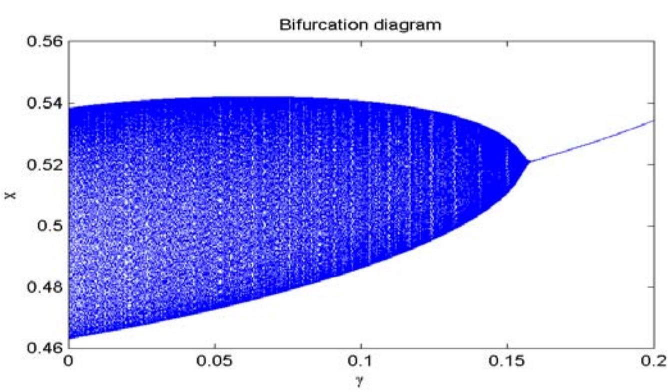

FIG. 4.5. *Bifurcation diagram of system* (1.2) *in terms of* γ *with* $b = 1.94884, h = 0.125, u = 4e, d = 2.05, r = 1,$ *and initial value* $(x_0, y_0) = (0.49, 0.67)$.

always attracted into the invariant torus whenever the initial densities are located in the attraction basin of the stable limit cycle of Figure 3.1(b) and the amplitude of the periodic harvesting $\gamma < 0.6$. The invariant torus is turned into a periodic orbit when $\gamma > 0.6$ (see Figures 4.4(a), (b), and (c)).

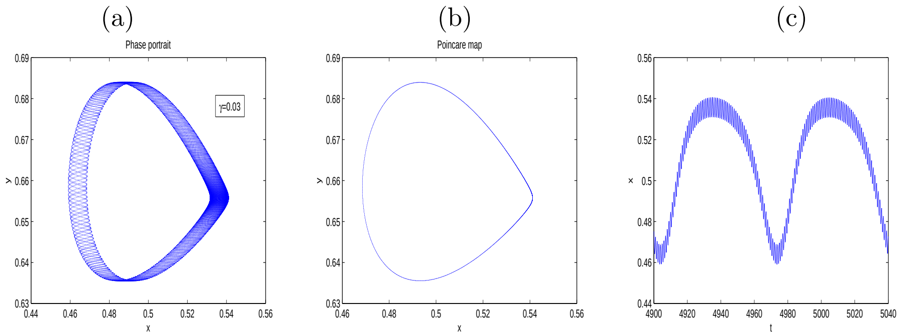

FIG. 4.6. (a) *Phase portrait for* $\gamma = 0.03$ *in Figure* 4.5. (b) *An attractor of the Poincaré map corresponding to* (a). (c) *The time series of the prey corresponding to* (a).

4.3. Bifurcation of stable homoclinic loops into invariant homoclinic tori. In Figure 3.4(e), there exists a stable homoclinic loop. Now we plot the bifurcation diagram of system (1.2) with $r = 1$ in the (γ, x)-plane in Figure 4.5, where the other parameter values are the same as those in Figure 3.4(e), that is, $b = 1.94884, h = 0.125, u = 4e$, and $d = 2.05$. We choose the initial density as $(x_0, y_0) = (0.49, 0.67)$, which is located in the attraction basin of the stable homoclinic cycle of Figure 3.4(e). The phase portrait, the attractor of the Poincaré map, and the time series for $\gamma = 0.03$ in Figure 4.5 are shown in Figures 4.6(a), (b), and (c), respectively, from which we can see that the stable homoclinic cycle in Figure 3.4(e) is bifurcated into an attracting invariant homoclinic torus in Figure 4.6.

5. Discussion. We first showed that numerous kinds of bifurcation phenomena occur in model (1.2) with only constant-yield prey harvesting, including saddle-node bifurcation, degenerate Hopf bifurcation, and Bogdanov–Takens bifurcation (i.e., cusp bifurcation of codimension 2), as the model parameters vary. These results reveal far richer dynamics compared to the model with no harvesting. We then considered system (1.2) with seasonal prey harvesting. Sufficient conditions on the existence of an asymptotically stable periodic solution and bifurcation of a stable periodic orbit into an invariant torus were given. Numerical simulations of the model (1.2) with seasonal prey harvesting, including bifurcation diagrams, phase portraits, and Poincaré maps, were carried out. It was shown that the model undergoes bifurcations from a hyperbolic stable equilibrium to a stable limit cycle, from a stable periodic solution to an invariant torus, and from a stable homoclinic loop to an invariant homoclinic torus, respectively, as the amplitude of seasonal harvesting increases.

In [6], Brauer and Sánchez have shown that in autonomous single population models, the behaviors of the model with periodic harvesting are analogous to those of the model with no harvesting, but with an asymptotically stable periodic solution instead of an asymptotically stable equilibrium. However, little is known about periodic harvesting of interacting populations [6]. Here, we have shown that similar conclusions hold for predator-prey models as long as the initial species densities are chosen suitably, but with an attracting invariant torus instead of a stable limit cycle.

The analytical and numerical results in this paper demonstrate that the initial species densities are very important for the persistence of the interacting species when the prey species is subjected to periodic harvesting. In order to have the long term

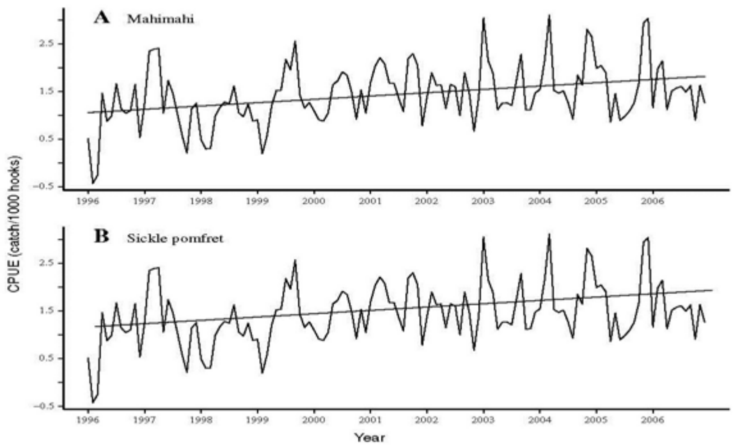

FIG. 5.1. *Temporally and spatially adjusted monthly catch per* 1000 *hooks and linear trend lines from the generalized additive models for those species exhibiting quasi-periodic patterns in the Hawaii deep-set longline fishery,* 1996-2006: (A) *Mahimahi (Coryphaena hippurus), and* (B) *sickle pomfret (Taractichthys steindachneri) (from Polovina et al.* [31]*, courtesy of the National Oceanic and Atmospheric Administration (NOAA) and the Department of Commerce).*

survival of the interacting species with seasonal harvesting in the form of a stable periodic solution or stable quasi-periodic solutions, the initial species densities must locate in the attraction basin of the stable attractor (hyperbolic stable equilibrium, stable limit cycle, or stable homoclinic loop) in the model with no harvesting or with constant-yield harvesting. These results also indicate that the dynamical behaviors of the model are very sensitive to the constant-yield or seasonal prey harvesting and careful management of resource and harvesting policies is required in the applied conservation and renewable resource contexts. Notice that the unharvested model describes the group defense phenomenon in predator-prey interactions; that is, when the density of the prey population is sufficiently large, the predation by predators is reduced, and their survival becomes difficult (Xiao and Ruan [39]). The results of this study show that appropriate seasonal harvest on the prey population can stabilize the system such that both the prey and predators coexist in the form of periodic or quasi-periodic solutions.

As seen in Figure 1.1, average monthly fishing effort in the deep-set fishery showed seasonal patterns from 1996 to 2006. Polovina et al. [31] used a generalized additive model to fit both the linear trend and seasonal components of monthly catch-per-unit-effort (CPUE), measured as the number of fish caught per 1000 hooks, exhibiting quasi-periodic trends for many of the top 10 species over the 1996–2006 period (see Figure 5.1 for data on two species). It would be interesting to modify our model and apply the obtained results to simulate such fishery data. We also would like to mention that we numerically showed only the bifurcation from a stable homoclinic orbit to an invariant homoclinic torus in model (1.2). The theoretical analysis of such a bifurcation remains open.

Acknowledgments. We would like to thank Professors Chris Cosner, Hüseyin Koçak, and Kening Lu for helpful discussions. We also thank the two anonymous referees for their valuable comments and suggestions.

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