Dynamics of Stage-structured Population Models with Harvesting Pulses

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Abstract In most models of population dynamics, changes in population due to birth or harvesting are assumed to be time-independent, but many species reproduce or are caught only during a single period of the year. In this paper a single species stage-structured model with density-dependent maturation rate, birth pulse and harvesting pulse is formulated. Using the discrete dynamical system determined by its Poincare map, the existence and stability of nonnegative equilibrium is studied. Furthermore by simulation，a detailed study of the various dynamics are made including period doubling, period halfing, intermittency, crisis, nonunique dynamics and chaotic attractors. The occurrence of these complex dynamic behaviors is related to the fact that minor changes in parameter or initial values can strikingly change the dynamic behaviors of the system. Finally, the dynamic behavior of the system is compared when μ is used as a bifurcation parameter with that when b is used.

Key-Words: Stage structure, Density-dependent, Harvesting pulse, Birth pulse, Complexities.

1 Introduction

The description of the age structure of the population in the life history is an interesting problem in population dynamics, since in the natural world; there are many species whose individual members exhibit enormous diversity. Metamorphosis may carry the same individual through several totally different niches during a lifetime. Specialized stages may exist for dispersal or dormancy. And the vital rates (rates of survival, development, and reproduction) almost always depend on age, size, or development stage.

Stage structure models have received much attention in recent years. There has been a fair amount of previous work on modeling with various stages of life history using continuous and discrete models. For example, TOMAD [1] gave two models to account for the dynamics of a consumer-resource system in which the consumers are divided into juveniles and adults; Zhang and Chen [2] established a stage-structured predator-prey model and investigated optimal harvesting policy; Wang [3] established a predator-prey model with stage structure for the predator which improves the assumption that each individual predator has the same ability to capture prey. It is assumed that immature individuals and mature individuals of the predator are divided by a fixed age and that immature predators do not have the ability to attack prey; Lu and Chi [4] established a nonautonomous stage-structured single-species dispersal model with harvesting of mature individuals in an N-patch environment, in which the individual members of the population have a life history that takes them through two stages：immature and mature; Ou and Luo [5] considered an autonomous predator-prey system in which individuals in the population may belong to one of two classes: the immature and the matures，and the age to maturity is represented by a time delay; Derik and Jorge[6] studied the coexistence in a competitive parasite-host system with a stage-structured host; Bo and Yasuhiro[7] have proposed and studied a stage-structured population with two life stages, immature and mature, exposed to environmental hormone which is stored in the bodies for an interval τ and gives damage to the reproductive ability of the population; Xiao and Chen [8] considered the dynamical behavior of a stage-structured SIR infectious disease model. This is not only because they are much simpler than the models governed by partial differential equations but also they can exhibit phenomena similar to those of partial differential models, and many important physiological parameters can be incorporated.

In above models it is invariably assumed that the mature reproduce or are harvested throughout the year, whereas it is often the case that births are seasonal or occur in regular pulses. The continuous reproduction (or harvest) of mature population is then removed from the model, and replaced by an annual birth pulse (or impulsive harvest). These models are subject to short-term perturbations which are often assumed to be in the form of impulses in the modeling process. Consequently, impulsive differential equations provide a natural description of such systems [9-11]. Equations of this kind are found in almost every domain of applied sciences. Numerous examples are given in Bainov's and his collaborator's book [10]. Some impulsive equations have been recently introduced in population dynamics in relation to: vaccination [12-14], chemotherapeutic treatment of disease [15, 16], impulsive birth [17, 18] and biological impulsive control [19-22].

In this paper, a stage-structured population model with pulse birth and pulse harvest of adult species is studied. It is supposed that the life history of the species is divided into two stages (immature and mature) and the maturity rate of juveniles is density dependent. The purpose of this paper is to study the effects of pulse harvesting rate and birth rate on dynamics of this model. In terms of the mathematical treatment, the presence of impulses gives the system a mixed nature, both continuous and discrete. The qualitative properties of the system are embodied in those of the discrete system which determines the state after a pulse in terms of the state after the previous pulse. Thus, in section 3, we deduce the stroboscopic map, where the map determines the number of immature population and mature population, immediately after each pulse birth at the discrete time m (m is a positive integer). When the birth rates of mature population are influenced by the population density, the discrete dynamical system determined by the stroboscopic map becomes nonlinear. The population in the pulsed birth and harvest time is characterized not by an exponential growth rate, but by the existence and stability of equilibria, by the bifurcations that occur when stability is lost, and by the patterns of dynamics (cycles, chaos) that follow the bifurcations.

2 Model formulation

Suppose that a population is divided into the class of juveniles denoted by $x(t)$, and that of adults denoted by $y(t)$. Juveniles are incapable of reproducing. To understand the effects of the competition between juveniles and adults, it is assumed that the dependence of vital rates on the population density is through a dependence upon a weighted total population size

$$W(t) = \alpha x(t) + y(t) , \qquad (1)$$

where the competition coefficient $\alpha > 0$ measures the competition effects. Then, the dynamics of the population is governed by the following system of equations

$$\begin{cases} x'(t) = B(W)y - (S(W) + D_1(W))x, \\ y'(t) = S(W)x - D_2(W)y. \end{cases} \qquad (2)$$

The biological implications of all functions in equation (2) are illustrated by [23]. The dependence of vital rate on population density (rates of survival, death, and reproduction) found in biological literature is known as the Ricker function:

$$G(W) = be^{-aW}, \qquad a > 0, b > 0.$$

The dynamic behavior of model (2) is characterized by the equilibria, periodic solutions [23-25].

One of the main purposes of this paper is to study how the density-dependent maturity rate of juveniles affects dynamical behaviors of system (2) with birth pulses and harvesting pulse. For simplicity, one takes

$$b(W) = b, D(W) = D(W) = d, S(W) = ae^{-W}$$

with $\alpha = 1$.

Let us consider

$$\begin{cases} x'(t) = -dx(t) - ax(t)e^{-W(t)}, t \neq m \\ y'(t) = ax(t)e^{-W(t)} - dy(t), t \neq m \\ x(m^+) = x(m) + by(m), t = m \\ y(m^+) = y(m) - \mu y(m), t = m \end{cases} \qquad (3)$$

where $W(t) = x(t) + y(t)$, and m is a positive integer. The parameter μ ($\in [0,1]$) represents the fraction of adults which is harvested at m. Positive d is the death rate constant. The maturity rate is $ae^{-W(t)}$, and b is the birth rate of mature population.

3 Dynamic behaviors

In the following, the stability of equilibria of system (3) and bifurcation are investigated.

3.1 Poincare map of system (3).

Adding the first two equations of (3), one gets

$$x(t) + y(t) = (x_m + y_m)e^{-d(t-m)}, m \le t < m+1 \quad (4)$$

where x_m and y_m are the initial population of juveniles and adults at time m respectively. Substituting (4) into the first equation of system (3) gives the expression of the juvenile population between pulses (i.e. $m \le t < m+1$).

$$x(t) = x_m \exp[-d(t-m) + a(E_i(1, x_m + y_m) - E_i(1,, x_m + y_m)e^{-d(t-m)}))/d]. \quad (5)$$

The exponential integral $E_i(n, x)$, where n is a nonnegative integer, are defined

$$E_i(n, x) = \int_1^\infty \frac{e^{-tx}}{t^n} dt$$

and is extended by analytic continuation to the entire complex plane with the exception of the point 0 in the case of $E_i(1, x)$. For more details on exponential integral function $E_i(1, x)$, one can see the reference [26].

From (4) and (5) one has

$$\begin{cases} x(t) &= x_m \exp[-d(t-m) + a(E_i(1, x_m + y_m) \\ & \quad - E(1, (x_m + y_m)e^{-d(t-m)}))/d], \\ y(t) &= (x_m + y_m)e^{-d(t-m)} - x_m \exp \\ & \quad [-d(t-m) + a(E_i(1, x_m + y_m) \\ & \quad - E(1, (x_m + y_m)e^{-d(t-m)}))/d], \\ & \quad m \le t < m+1. \end{cases} \quad (6)$$

Equations (6) hold between pulses and at each successive pulse, more of the juvenile population is added and the adult population is caught. Then we have

$$\begin{cases} x_{m+1} = bp(x_m + y_m) + p(1-b)x_m \\ \qquad \exp[aH(x_m + y_m)/d] \\ \\ y_{m+1} = bp(x_m + y_m) - pqx_m \\ \qquad \exp[aH(x_m + y_m)/d] \end{cases} \quad (7)$$

where $p = e^{-d}, q = 1 - \mu$, and

$$H(x_m + y_m) = E_i(1, x_m + y_m) - E_i(1, p(x_m + y_m)).$$

System (7) is a discrete system. It describes the numbers of juvenile population and adult population at a pulse in terms of values at the previous pulse. The dynamic behaviours of system (7) coupled with (6) determines the dynamical behaviours of system (3). Thus, in the following sections, we will pay our attention

on system (7) and investigate the various dynamical behaviours. The dynamics of the nonlinear system (7) can be studied as a function of any of parameters. We will focus here on μ (or b) and document the changes in the qualitative dynamics of the model (7) as μ (or b) varies. In order to study the stability of equilibria of system (7) the following lemma [26] is necessary.

Lemma 3.1 The functions $E_i(1, x)$ and $H(x)$ have the following properties:

(i)The 1-argument exponential integral is a Cauchy Principal Value integral, defined only for real arguments x, as follows

$$Ei(x) = \int_{-\infty}^x e^t / t \, dt$$

and for $x < 0$,

$$Ei(x) = -Ei(1, -x);$$

(ii) The Maclaurin expansion of $Ei(x)$ is given by

$$Ei(x) = \gamma + \ln(x) + \sum_{n=1}^\infty \frac{x^n}{n!}, x > 0$$

where γ is Euler's constant [26]. This shows that $Ei(x)$ can be approximated with a logarithm in the vicinity of zero;

(iii) $\lim_{x \to 0} H(x) = -d$ and $\lim_{x \to \infty} H(x) = 0$ for any fixed $p \in (0,1]$;

(iv) $H'(x) = \dfrac{e^{-px} - e^{-x}}{x} > 0$ and $-d \le H(x) \le 0$ for $x > 0$.

3.2 Stability of equilibria of system (7).

From Lemma 3.1, in the neighborhood of $(x, y) = (0,0)$, the dynamics of equations (7) is governed by the linearization equation

$$X_{m+1} = AX_m, \quad (8)$$

where

$$A = \begin{pmatrix} bp + (1-b)pe^{-a} & bp \\ \\ pq - pqe^{-a} & pq \end{pmatrix}$$

and $X = (x, y)^T$. For the stability of $(x, y) = (0,0)$ of system (7), one has the following result.

Theorem 3.1. If $\mu > \mu_0$, then the equilibria $(x, y) = (0,0)$ is stable.

Proof: $X = 0$ is stable when the eigenvalues of A are less than one in magnitude. This is true only when A satisfies the three Jury conditions.

$$P1 = 1 - trA + \det A > 0 \qquad (9a)$$

$$P2 = 1 + trA + \det A > 0 \qquad (9b)$$

$$P3 = 1 - \det A > 0 \qquad (9c)$$

It can be shown that inequalities (9b) and (9c) are always satisfied, and that as μ decreases, inequality (9a) is violated at a critical point μ_0:

$$\mu_0 = \frac{p - p^2 e^{-a} - 1 + pe^{-a} - bpe^{-a} + bp}{p - p^2 e^{-a}}.$$

Remark 1. From a biological point of view, it is reasonable that $0 \le \mu_0 \le 1$. Hence we constrain

$$\mu_0 = \frac{(1-p)(1-pe^{-a})}{p(1-e^{-a})} \le b \le \frac{1-pe^{-a}}{p(1-e^{-a})}.$$

In order to prevent population from extinction, μ must be less than μ_0. That is, if $\mu > \mu_0$, the population goes to extinction.

In the rest of this section, we assume $\mu < \mu_0$ and look for positive equilibrium $E(x^*, y^*)$ of system (7), which satisfies

$$\begin{cases} x = bp(x+y) + p(1-b)xe^{aH(x+y)/d} \\ \\ y = pq(x+y) - pqxe^{aH(x+y)/d} \end{cases} \qquad (10)$$

For the existence and stability of $E(x^*, y^*)$ of system (7), one obtained result as follows.

Theorem 3.2. If $\mu < \mu_0$ and $b > \mu + 1/p^2 - 1$, there is a unique interior fixed point $E(x^*, y^*)$ for system (7). There exists a surface $\mu_c(p,d,a)$ in the parameter space so that if $\mu_c(p,d,a) < \mu < \mu_0$, then $E(x^*, y^*)$ is locally stable, and if $\mu > \mu_c(p,d,a)$, then $E(x^*, y^*)$ is a flip bifurcation when μ is used as a bifurcation parameter.

Proof: It follows from the second equation of (10) we have

$$y = \frac{pq}{1-pq}(1 - e^{aH(x+y)/d})x \qquad (11)$$

Adding x to both sides of (11), one has

$$x = \frac{(1-pq)W}{1 - pq\exp(aH(W)/d)} \doteq f(W)$$

where $W = x + y$.

Again from the second equation of (10) we have

$$pqW = y + pqx\exp(aH(W)/d). \qquad (12)$$

Substituting (12) into the first equation of (10) and using (11), one has

$$\exp(aH(W)/d) = \frac{bp - 1 + pq}{bp - p + p^2 q},$$

$$x = \frac{b - 1 + pq}{b - 1 + q}W \doteq g(W) \qquad (13)$$

If

$$b > \mu + \frac{1}{p^2} - 1 \ge \mu + \frac{1}{p} - 1$$

and

$$b - 1 + pq > bp - 1 + pq > 0,$$

then

$$0 < \frac{bp - 1 + pq}{bp - p + p^2 q} < 1.$$

By Lemma 3.1, it follows that $f(W) > 0$ for $W > 0$ and

$$f(W) = (1-pq)\left\{ \frac{(1 - pa\exp(aH(W)/d))}{[1 - pq\exp(aH(W)/d)]^2} \right.$$
$$\left. + \frac{\frac{apq}{d}\exp(aH(W)/d)WH'(W)}{[1 - pq\exp(aH(W)/d)]^2} \right\} \qquad (16)$$

According to the properties of $H(W)$, we have $f'(W) > 0$ for $W > 0$ and

$$f'(0) = \frac{1-pq}{1 - pqe^{-a}}. \qquad (15)$$

Thus from (13),(15), $\mu < \mu_0$ and

$$b > \mu + \frac{1}{p^2} - 1 \ge \mu,$$

one has

$$f'(0) - g'(0) = \frac{1-pq}{1 - pqe^{-a}} - \frac{b - 1 + pq}{b - 1 + q}$$
$$= \frac{q[(1-pq)(1-pe^{-a}) - bp(1-e^{-a})]}{(1 - pqe^{-a})(b + q - 1)} < 0. \qquad (16)$$

On the other hand, by the expressions of $f(W)$ and $g(W)$ one has

$$f(W) - g(W) =$$

$$W\left[\frac{1-pq}{1-pq\exp(aH(W)/d)} - \frac{b-1+pq}{b-q-1}\right]$$

$$\doteq WD(W).$$

where

$$D(W) = \frac{1-pq}{1-pq\exp(aH(W)/d)} - \frac{b-1+pq}{b-q-1}.$$

By the property (iii) of function H one has

$$\lim_{W \to \infty} D(W) = \frac{q(1-p)}{b+q-1} > 0, \ p \in (0,1].$$

This shows that the curve $f(W)$ lies above the curve $g(W)$ as w is sufficiently large. Since both functions are continuous, the graphs of the functions f and g intersect once. This implies that system (7) has a unique fixed point $E(x^*, y^*)$ in the interior of R_2^+ if $\mu < \mu_0$ and $b > \mu + \frac{1}{p^2} - 1 \geq \mu$.

For the stability of the fixed point $E(x^*, y^*)$ of system (7), we equivalently consider the following system

$$\begin{cases} x_m = bpW_m + p(1-b)x_m \exp(aH(W_m)/d) \\ W_{m+1} = p(q+b)W_m + p(1-b-q)x_m \\ \qquad \exp(aH(W_m)/d) \end{cases} \quad (17)$$

Let

$$A_{11} = p(1-b)\exp(aH(W^*)/d),$$

$$A_{12} = bp + \frac{ap(1-b)x^*}{d}H'(W^*)\exp(ah(W^*)/d),$$

$$A_{21} = p(1-b-q)\exp(aH(W^*)/d),$$

$$A_{22} = p(q+b) +$$

$$\frac{ap(1-b)x^*}{d}H'(W^*)\exp(aH(W^*)/d).$$

The Jacobian matrix of system (17) at $E(x^*, y^*)$ is given by

$$A = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix} \quad (18)$$

It follows from (9) that we have

$$P1 = 1 - [p(1-b)\exp(aH(W^*)/d) + p(q+b) +$$

$$\frac{ap(1-b)x^*}{d}H'(W^*)\exp(aH(W^*)/d)] +$$

$$p^2q\exp(aH(W^*)/d),$$

$$= \frac{a(bp-1+pq)}{d}W^*H'(W^*)$$

$$P2 = 1 + [p(1-b)\exp(aH(W^*)/d) + p(q+b) +$$

$$\frac{ap(1-b)x^*}{d}H'(W^*)\exp(aH(W^*)/d)] +$$

$$p^2q\exp(aH(W^*)/d)$$

$$= 1 + pq + pd + \frac{(bp-1+pq)(1-b+pd)}{b-1+pq} -$$

$$\frac{a(bp-1+pq)}{d}W^*H'(W^*),$$

$$P3 = 1 - p^2q\exp(aH(W^*)/d).$$

By the properties of function H and

$$b > \mu + \frac{1}{p^2} - 1 \geq \mu + \frac{1}{p} - 1,$$

it can be shown inequalities $P1 > 0$ and $P3 > 0$ are always satisfied. If inequality $P2 > 0$ is violated, i.e.,

$$W^*H'(W^*) > \frac{2d(b-1+bp^2q+p^2q^2)}{a(bp+pq-1)(b-1+pq))} \quad (19)$$

then A has an eigenvalue less than -1. We note that

$$b > \mu + \frac{1}{p^2} - 1 \geq \mu,$$

which implies

$$b - 1 + bp^2q + p^2q^2 > 0.$$

Now if we choose μ as the bifurcation parameter, then we can use the following equation to determine the bifurcation value $\mu_c(p,b,a)$:

$$W^*H'(W^*) = \frac{2d(b-1+bp^2q+p^2q^2)}{a(bp+pq-1)(b-1+pq)}. \quad (21)$$

This shows that the bifurcation at $\mu_c(p,b,a)$ is a flip bifurcation if μ is used as a bifurcation parameter.

Remark 2. From a biological point of view and Remark 1, there is a unique interior fixed point $E(x^*, y^*)$ for the system (7) if

$$\max\left\{\frac{(1-p)(1-pe^{-a})}{p(1-e^{-a})}, \mu + \frac{1}{p^2} - 1\right\}$$

$$\leq b \leq \frac{1-pe^{-a}}{p(1-e^{-a})}$$

and $\mu < \mu_0$.

If we choose b as the bifurcation parameter, then the following corollary holds.

Corollary. If $b > b_0$, where

$$b_0 = \frac{(1-pq)(1-pe^{-a})}{p(1-e^{-a})}$$

there is a unique interior fixed point $E(x^*, y^*)$ for the system (7). There exists a surface $b_c(p,q,a)$ in the parameter space so that if $b_0 < b < b_c(p,q,a)$, then $E(x^*, y^*)$ is locally stable, where $b_c(p,q,a)$ is determined by (21). If $b > b_c(p,q,a)$, then $E(x^*, y^*)$ is unstable. The bifurcation at $b = b_c(p,q,a)$ is a flip bifurcation if b is used as the bifurcation parameter.
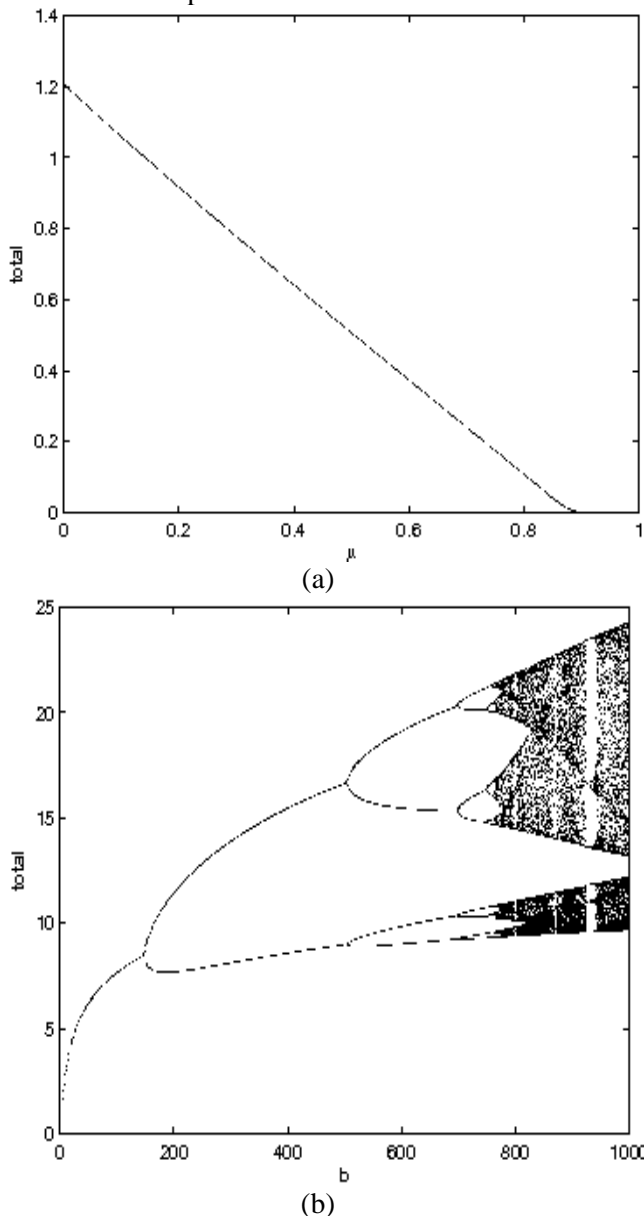

(a)

(b)

Figure 1: (a) The existence of equilibria (0,0) and (x^*, y^*) for system (7). When $\mu > 0.8812$, equilibrium (0,0) is stable; when $\mu < 0.8812$, there exists a positive equilibrium (x^*, y^*), where d=0.99, a=0.9, b=3.68, $x(0)$=1 and $y(0)$=1. (b)

Bifurcation diagrams of equation (7) for total population which shows the effect of parameter b on the dynamical behavior of system (7) with d=0.99, a=0.9, μ=0.6, $x(0)$=1, $y(0)$=1.

4. Complexity analysis

The focus so far has been on the equilibria of the system (7), and in particular, on the existence and stability of those equilibria (see Fig. 1(a)). But if the conditions of theorems 3.1 and 3.2 are invalid, equation (7) exhibits a wide variety of dynamical behaviors.

4.1 Period doubling and period halfing

In Fig.1 (b), the bifurcation diagrams for model are displayed (7). After the first flip bifurcation, the model undergoes a series of period-doubling bifurcations wherein a 2^k-cycle loses stability and a stable 2^{k+1}-cycle is born as b increases. Successively higher periods are stable for smaller ranges of b. Eventually, chaotic dynamics set in. This period doubling route to chaos is the hallmark of logistic and Ricker maps[27,28] and has been studied extensively by mathematicians [29,30]. Fig.3(a) and (b) display period-doubling sequences.

Fig.2 (a) is followed by a cascade of periodic halfing bifurcations from chaos to 3-periodic solution when $\mu > 0.4$. Fig.2 (b) is followed by a cascade of periodic halfing bifurcations from chaos to chaos solution between $\mu = 0.4$ and $\mu = 0.8$. The phase portrait of a chaos is shown in Fig.4(a).
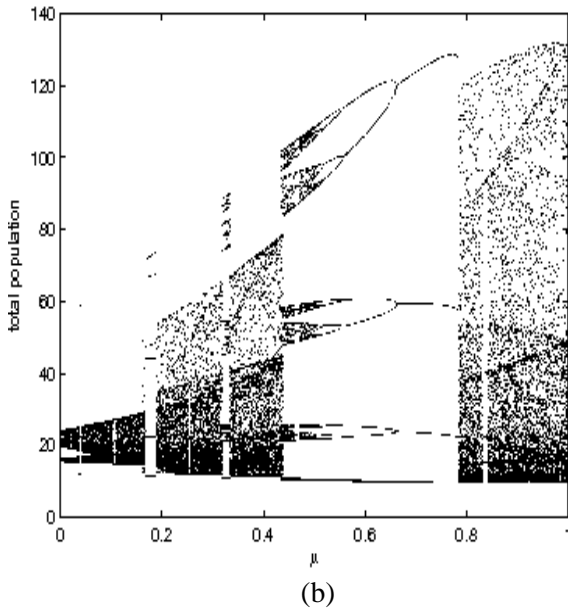

(a)

(b)
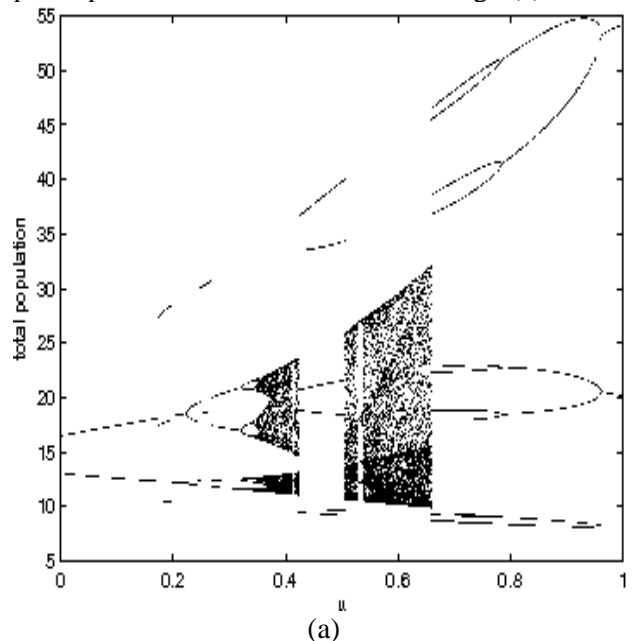
Figure 2: Bifurcation diagrams of equation (7) for total population with respect to parameter μ, where d=0.99, a=0.9, $x(0)$=9 and $y(0)$=3. (a) b=1500. (b) b=6000.
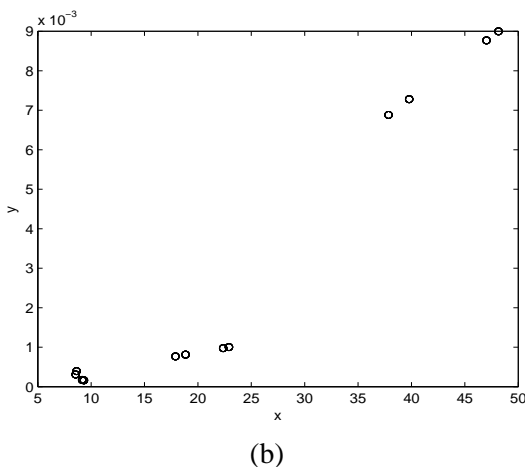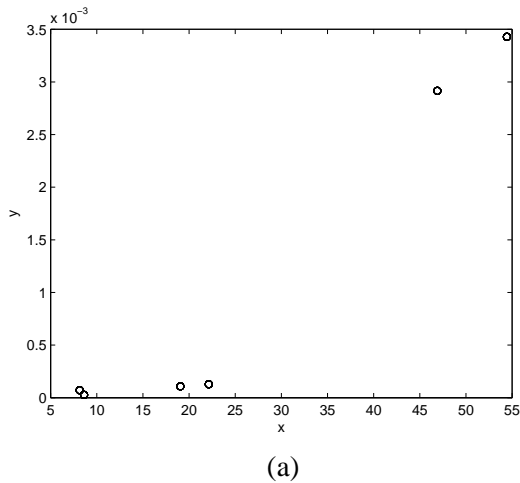

(a)

(b)

Figure 3: The period-doubling sequences, where d=0.99, a=0.9, $x(0)$=9, $y(0)$=3. (a) A six-cycle with μ =0.42. (b) A twelve-cycle with μ =0.7.

4.2. Intermittency and crisis.

we remark on intermittency and crises. The intermittency route to chaos is characterized by dynamics with irregularly occurring bursts of chaotic behavior interspersed with intervals of apparently periodic behavior. A crisis is a bifurcation event in which a chaotic attractor and its basin of attraction suddenly disappear or suddenly change in size as some control parameter is adjusted, a phenomenon which was first extensively analyzed by Grebogy et al.[31]. Such an occurrence is an example of a crisis. When the parameter μ is slightly increased in Fig. 2(b), the chaotic attractor abruptly disappears or changes its size, thus constitutes a type of attractor crises.

4.3. Nonunique attractors.

Reviewing the bifurcation diagram for the total population in Fig. 2, we see that sudden changes from one type of an attractor to another do occur quite often. One obvious change occurs in the vicinity of $\mu = 0.5$, the solution from period-6 turns to chaos in Fig.2 (a). Here a period-2 attractor changes to an attractor which shows period-3 type dynamics in the vicinity of $\mu = 0.19$. A more detailed numerical analysis reveals that the question is not only about windows of frequency-locking or periodic windows in the middle of chaos. Instead, it appears that the attractor is nonunique: in this case the alternative attractors are, for example, a chaos attractor changes to four chaos attractors when $\mu = 0$ in Fig.2 (b). The phase portrait of a four chaos attractors is shown in Fig.4 (b). Multiple attractors are known to be possible, and probably common, in nonlinear discrete-time matrix population models [32].

5. Discussion

In this paper, a stage-structured single species model with birth pulse and harvesting pulse and density dependent maturation rate is proposed and investigated. It is shown that the system exhibits stable nonnegative equilibria if some conditions are satisfied. Furthermore if those conditions are invalid, equation (7) exhibits a wide variety of dynamical behaviors. If the bifurcation parameters μ and b have different choice for system (3), then the conditions of the existence and stability of nonnegative equilibria are different.

(1) From Remarks 1, 2 and biological point of view, we know that if we choose μ as the bifurcation parameter, the conditions of the existence and stability of nonnegative equilibria are

dependent on parameter b. In order to keep the biological meaning of $\mu_0 (0 \le \mu_0 \le 1)$, we constrain

$$\frac{(1-p)(1-pe^{-a})}{p(1-e^{-a})} \le b \le \frac{1-pe^{-a})}{p(1-e^{-a})}$$

Condition $b > \mu + \dfrac{1}{p^2} - 1$ is set to keep the existence of positive equilibria. However, by Corollary we know that if we choose b as the bifurcation parameter, the conditions of the existence and stability of nonnegative equilibria are only dependent on parameter b_0.

(2) The results of Theorems 3.1, 3.2 and Corollary are in line with reality from a biological point of view. That is μ (or b) must be less (or larger) than $\mu_0 (or b_0)$ in order to prevent population from extinction.

Another hand, it is interesting to compare the stage-structured model analyzed here, which has a harvesting pulse, with the analogous stage structured model which has no harvesting [32]. The threshold value

$$b_0 = \frac{(1-p)(1-pe^{-a})}{p(1-e^{-a})}$$

and the bifurcation point $bc(p; q; a)$ in model (3) has relation with $\mu(q = 1 - \mu)$. However, the threshold value and the bifurcation point are

$$\overline{b}_0 = \frac{(1-p)(1-pe^{-a})}{p(1-e^{-a})}$$

and $bc(p; a)$, respectively. Obviously, b_0 is larger than $\overline{b}_0$, which is in line with reality from a biological point of view . That is, if population is exploited, the rate of pulse birth should be larger in order to prevent population from extinction.

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