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ORIGINAL PAPER

Complex dynamics of survival and extinction in simple population models with harvesting

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Abstract We study the effects of constant harvesting in a discrete population model that includes density-independent survivorship of adults in a population with overcompensating density dependence. The interaction between the survival parameter and other parameters of the model (harvesting rate, natural growth rate) reveal new phenomena of survival and extinction. The main differences with the dynamics of survival and extinction reported for semelparous populations with overcompensatory density dependence are that there can be multiple windows of extinction and conditional persistence as harvesting increases or the intrinsic growth rate is increased, and that, in case of bistability, the basin of attraction of the nontrivial attractor may consist of an arbitrary number of disjoint connected components.

Keywords Extinction · Persistence · Discrete dynamical system · Bifurcation · Bimodal map

Introduction

Populations subject to harvesting or migration may exhibit counterintuitive effects such as the *hydra effect* (Abrams 2009), or *unusual extinction* (Sinha and Parthasarathy 1996). The first one refers to the fact that harvesting may increase stock size, while the paradoxical effect of unusual extinction means that populations can persist within a band of high depletion, whereas extinction occurs for lower depletion rates. This phenomenon is linked to one-dimensional discrete models with constant harvesting, and it was uncovered by Sinha and Parthasarathy (1996). Further study, as well as very interesting references to dramatic examples of abrupt changes in the stock of some populations, can be found in Sinha and Das (1997), Vandermeer and Yodzis (1999), and Schreiber (2001).

In the above quoted references, the unusual behavior under the influence of harvesting was studied in well-known, discrete, single-species models for the growth of semelparous populations with overcompensating density dependence of the form

$$x_{n+1} = f(x_n), \tag{1}$$

where x_n is the population size of a species in the generation n and the continuous function $f : [0, \infty) \to [0, \infty)$ reflects the nonlinear density growth. This simple model assumes that all individuals have equal influence on the size of the population in the following year, and it is usually applied to semelparous organisms with nonoverlapping generations (May 1974; Clark 1990). Three famous choices of the recruitment function f are the quadratic map $f(x) = rx(1 - x)$, the Ricker function $f(x) = x \exp(r(1 - x))$, and the generalized Beverlton–Holt map $f(x) = rx/(1 + x^{\gamma})$. The latest one is also referred to as the Bellows map after his famous paper (Bellows 1981), in which its flexibility and good descriptive properties are emphasized.

As far as we know, the most thorough result on the influence of a constant harvesting on the dynamics of this kind of model is due to Schreiber (2001). He considers a family of equations that essentially have the

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form $x_{n+1} = \max\{f(x_n) - d, 0\}$, where d is a constant meaning harvesting or migration, and the assumptions on f are general enough to include the three examples mentioned above.

Semelparous models assume that the adult population x_n dies during spawning and is replaced by the subsequent cohort of recruits $x_{n+1} = f(x_n)$. In this paper, we will focus on the influence of a constant harvesting on the dynamics of an iteroparous population with overcompensating density dependence. More precisely, we will consider equation

$$x_{n+1} = \alpha x_n + (1 - \alpha) f(x_n), \qquad (2)$$

where $\alpha \in [0, 1]$. We notice that the case $\alpha = 0$ corresponds to Eq. 1.

The main difference between Eqs. 1 and 2 is that, in the latest one, a probability of surviving the reproduction season is assumed. The parameter α can be interpreted as the fraction of energy invested into adult survivorship rather than reproduction. This interpretation assumes that density-dependent survivorship only acts on juveniles; this is the case of the Ricker model, which is based on the observation that certain species of fish as salmon habitually cannibalize their eggs and larvae. Actually, an interesting example of an ecological model governed by Eq. 2 is the Ricker difference equation as derived by Thieme (2003). Taking into account a density-dependent mortality rate of juveniles due to cannibalism, and a density independent mortality rate of adults, the following particular case of Eq. 2 is derived (for more details, see Appendix A):

$$x_{n+1} = \alpha x_n + (1 - \alpha) x_n e^{r(1-x_n)}. \qquad (3)$$

Here, x_n represents the (normalized) size of the population in year n immediately before the reproductive season, and α is an adult's probability of surviving 1 year, including the reproductive season.

Equation 2 has a rich history in the modeling of ecological systems with difference equations. For instance, it was employed in fishery models with a generalized logistic map $f(x) = rx(1 - x)^z$ (May 1980; Fisher 1984), and to describe the growth of bobwhite quail populations with f being the Bellows map (Milton and Bélair 1990).

Our main aim in this paper is to study the effect of constant harvesting on a population model governed by Eq. 2. That is, we will consider equation

$$x_{n+1} = \max\{\alpha x_n + (1 - \alpha) f(x_n) - d, 0\}, \qquad (4)$$

with $d \geq 0$. As far as we know, the dynamics of Eq. 4 have not been investigated before, although a related model was suggested by Clark (1976, p. 384) to determine the optimal equilibrium escapement level in a fishery model of Antarctic fin whales; a similar equation was employed as well by Allen and Keay (2004) to estimate annual change in the stock of Artic Bowhead whales.

The paper is organized as follows: In the section "The model without harvesting," we state the main assumptions and briefly describe some known properties of Eq. 2. The section "The influence of harvesting" is devoted to the analysis of the harvested model Eq. 4. Some mathematical material is placed in three appendices.

The model without harvesting

In this section, we briefly describe some qualitative properties of the solutions of Eq. 2.

First, we introduce some general properties and notation that will be used throughout the paper from now on. Unless explicitly stated, f will be a C^3 function satisfying the following properties:

(A1) f has only two fixed points: $x = 0$ and $x = K > 0$, with $f'(0) > 1$.

(A2) f has a unique critical point $c < K$ in such a way that $f'(x) > 0$ for all $x \in (0, c)$, $f'(x) < 0$ for all $x > c$.

(A3) $(Sf)(x) < 0$ for all $x \neq c$, where

$$(Sf)(x) = \frac{f'''(x)}{f'(x)} - \frac{3}{2}\left(\frac{f''(x)}{f'(x)}\right)^2$$

is the Schwarzian derivative of f.

(A4) $f''(x) < 0$ for all $x \in (0, c)$.

These assumptions are motivated by the paper of Schreiber (2001) and the fact that many maps usually employed in discrete population models fulfill them, in particular, the logistic and the Ricker maps for all $r > 0$ and the Bellows map for $r > 1$ and $\gamma \geq 2$.

For a given map f, and $\alpha \in [0, 1]$, we define the function $F_\alpha(x) = \alpha x + (1 - \alpha) f(x)$. The map F_α has exactly the same fixed points as f, that is, 0 and K.

One of the effects of increasing the parameter α in Eq. 2 is the stabilization of the equilibrium K (see Botsford 1992 for related discussions). The stabilizing effect of the parameter α can be easily proved. Indeed, assume that the discrete dynamical system generated by the recurrence Eq. 1 with a unimodal map f has an unstable positive fixed point K. This means that $f'(K) < -1$, and it is clear that $F'_\alpha(K) \in (-1, 1)$ for all $\alpha \in (\alpha_1, 1)$, where $\alpha_1 = (-1 - f'(K))/(1 - f'(K))$. Thus, a sufficiently big value of α stabilizes the positive equilibrium in the modified Eq. 2. Furthermore, it is not difficult to prove that, under conditions A1–A3, the positive fixed point is actually a global attractor of all positive solutions of Eq. 2 for $\alpha \geq \alpha_1$.

Sometimes, the shape of F_α does not change substantially between the cases $\alpha = 0$ and $\alpha > 0$. For example, the relation between the quadratic function $f(x) = rx(1-x)$ and the map $F_\alpha(x) = \alpha x + (1-\alpha) f(x)$ is only a rescaling of the parameter r after a change of variables. Indeed, the change $y = \beta x$ with $\beta = r(1-\alpha)/(r(1-\alpha)+\alpha)$ transforms equation

$$x_{n+1} = \alpha x_n + (1-\alpha) r x_n (1 - x_n) \tag{5}$$

into $y_{n+1} = R y_n (1 - y_n)$, with $R = r(1-\alpha) + \alpha$.

However, the situation for other unimodal functions such as the Ricker and the Bellows models is very different. In these cases, the modified map F_α can be bimodal (also called *hump-with-tail map*), see Fig. 1. This means that F_α has two critical points c_1, c_2, with $0 < c_1 < c_2$, in such a way that $F_\alpha(c_1)$ is a local maximum, and $F_\alpha(c_2)$ is a local minimum. See Appendix B for more details.

An important feature of the map $F_\alpha(x)$ in the bimodal case is that a floor beneath which the population cannot fall is created. Indeed, as noticed by Milton and Bélair, after transients have died out, population densities fall in the forward invariant interval $[F_\alpha(c_2), F_\alpha(c_1)]$, where c_1 and c_2 are, respectively, the critical points at which the local maximum and the local minimum of F_α are achieved. This floor not only helps to avoid complicated behavior, but also is very important to prevent the risk of extinction.

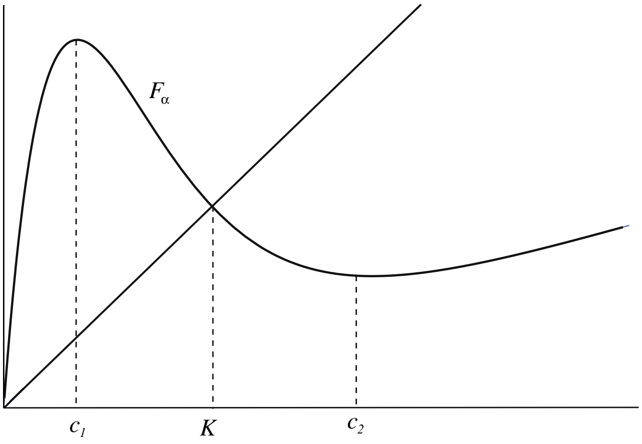

Fig. 1 Bimodal map $F_\alpha(x) = \alpha x + (1-\alpha) f(x)$, with $\alpha = 0.3$, $f(x) = x \exp(3(1-x))$

The influence of harvesting

In this section, we study Eq. 4, that is, the influence of constant harvesting in the dynamics of a population governed by Eq. 2.

For $\alpha \in [0, 1]$ and $d \geq 0$, we denote

$$F_{\alpha,d}(x) = \max\{\alpha x + (1-\alpha) f(x) - d, 0\}.$$

Assuming conditions A1–A2, it is clear that $F_\alpha(x) > x$ for all $x \in (0, K)$, and $F_\alpha(x) < x$ for all $x \in (K, \infty)$. If we further assume A4, then $F_{\alpha,d}$ can have at most three fixed points $0 < K_1 < K_2$ (this is an easy consequence of Rolle's theorem).

We adopt the terminology used by Schreiber to denote the three generic categories of the dynamics regarding extinction, namely:

- *Extinction:* The unique fixed point is $x = 0$, and it attracts all solutions of Eq. 4.
- *Essential extinction:* Not all solutions of Eq. 4 converge to zero, but a randomly chosen initial density leads to extinction with probability one.
- *Bistability:* There are two attractors: $\mathcal{A}_1 = \{0\}$, and $\mathcal{A}_2$. The basin of attraction of $\mathcal{A}_2$ is bounded away from zero, and it contains the initial values of the population for which it persists indefinitely.

Recall that, for a map g and an integer $k \geq 2$, g^k is defined as the kth iteration of g, that is, $g^2(x) = g(g(x))$, $g^3(x) = g(g(g(x)))$, and so on. A point z is periodic with prime period k for g if $g^k(z) = z$, and $g^i(z) \neq z$ for $1 \leq i \leq k-1$. In this case, the set $\{z, g(z), g^2(z), \ldots g^{k-1}(z)\}$ is called a cycle of period k.

An important result for the unimodal case is that the dynamics essentially depends on two facts: the number of fixed points of $F_{0,d}$ and the sign of $F^2_{0,d}(c) - K_1$, where c is the unique critical point of $F_{0,d}$. The transition from bistability to extinction occurs via a saddle-node bifurcation, after which the graph of $F_{0,d}$ lies below the line $y = x$ in the plane (x, y) for all $x > 0$. Therefore, the unique positive fixed point of $F_{0,d}$ is 0. On the other hand, a catastrophe bifurcation that takes place when $F^2_{0,d}(c) = K_1$ explains the transition between bistability and essential extinction. This mechanism can be viewed as a combination of overshooting the carrying capacity and the Allee effect (Gyllenberg et al. 1996).

The situation is much more complex for Eq. 4 in the bimodal case. Rather than giving an exhaustive analytical study, our aim here is to present the main differences with the unimodal case, with special attention to the new mechanisms for changing the modes of survival and extinction. However, for the quadratic map, a thorough study is possible. This is the content of the next subsection.

The quadratic map

Here, we discuss the quadratic case $f(x) = rx(1-x)$, which satisfies A1–A4 for all $r > 1$. As mentioned in the section "The model without harvesting," the map $F_\alpha = \alpha x + (1-\alpha)rx(1-x)$, $\alpha \in [0, 1)$, is still quadratic. Using this fact, the influence of the harvesting parameter d can be easily studied. We state the main results, which, in the particular case $\alpha = 0$, are in agreement with those of Schreiber (2001).

First, we notice that the map F_α has a unique critical point

$$c = \frac{\alpha + (1-\alpha)r}{2(1-\alpha)r}.$$

For $r > 1$ and $\alpha \in [0, 1)$, define

$$d_1 = d_1(\alpha, r) = \frac{(1-\alpha)(r-1)^2}{4r}$$

$$d_2 = d_2(\alpha, r) = \frac{-8 - 2r + r^2 + (r-1)^2(\alpha^2 - 2\alpha)}{4r(1-\alpha)}.$$

If $r \leq 1$ or $d > d_1$, then the unique fixed point of $F_{\alpha,d}$ is 0. Next, if $r > 1$ and $0 < d < d_1$, then there are two positive fixed points $K_1 < K_2$. Moreover, $F^2_{\alpha,d}(c) = K_1$ if and only if $\alpha < (r-4)/(r-1)$ and $d = d_2$. Thus, Theorem 1 in Schreiber (2001) allows us to prove the following result:

Proposition 1 *Consider Eq. 4 with* $f(x) = rx(1-x)$, $\alpha \in [0, 1)$, *and* $d \geq 0$. *The generic modes of survival/extinction are determined in the following way:*

(a) *Extinction: if* $r \leq 1$ *or* $d > d_1$, *then all orbits of Eq. 4 are attracted to the origin.*

(b) *Bistability: if* $r > 1$ *and* $d_2 < d < d_1$, *then there is an attracting interval bounded away from zero. Thus, populations can persist arbitrarily for some initial density values, while for others, the Allee effect leads to extinction.*

(c) *Essential extinction: it occurs if* $r > 1$ *and* $0 < d < d_2$.

We recall that, for $\alpha = 0$, essential extinction is only possible if $r > 4$ and $0 < d < d_2(0, r) = (-8 - 2r + r^2)/(4r)$. Since, for a fixed value of $r > 4$, the derivative of $d_2(\alpha, r)$ with respect to α is negative, and $d_2(\alpha, r) = 0$ for $\alpha = (r-4)/(r-1)$, there is a value $\alpha_1(r, d) < (r-4)/(r-1)$ such that essential extinction is avoided if the survivorship rate is greater than α_1.

As an example, we consider the case $r = 5$. When $\alpha = 0$, there is essential extinction for $d \in (0, 0.35)$, bistability for $d \in (0.35, 0.8)$, and extinction for $d > 0.8$.

Now, for $d \in (0, 0.35)$, we can compute the value of

$$\alpha_1 = \alpha_1(d) = \frac{1}{8}\left(8 - 5d - \sqrt{36 + 25d^2}\right),$$

such that there is bistability for Eq. 4 if $\alpha \in (\alpha_1, \alpha_2)$, where $\alpha_2 = \alpha_2(d) = (4 - 5d)/4$ is the value of α where the saddle-node bifurcation takes place. See Fig. 2a, where the survival/extinction diagram in the plane of parameters (α, d) is shown. In Fig. 2b, we plot the bifurcation diagram corresponding to $d = 0.2$. We choose the critical point c as the initial condition, and plot the iterates $f^n(c)$ for n between 250 and 300.

The catastrophe bifurcation leading from essential extinction to bistability takes place at the value $\alpha = (7 - \sqrt{37})/8 = 0.114655$, while the saddle-node bifurcation driving the system to extinction takes place for $\alpha = 0.75$.

We can interpret this result as follows: for a semelparous population with logistic growth, Schreiber proved that the paradoxical phenomenon of unusual extinction, as the harvesting pressure is increased, is observed if the growth rate is large enough ($r > 4$). If we fix a growth rate $r > 4$, the influence of harvesting for a iteroparous population governed by Eq. 5 with a small survivorship rate of adults α is qualitatively

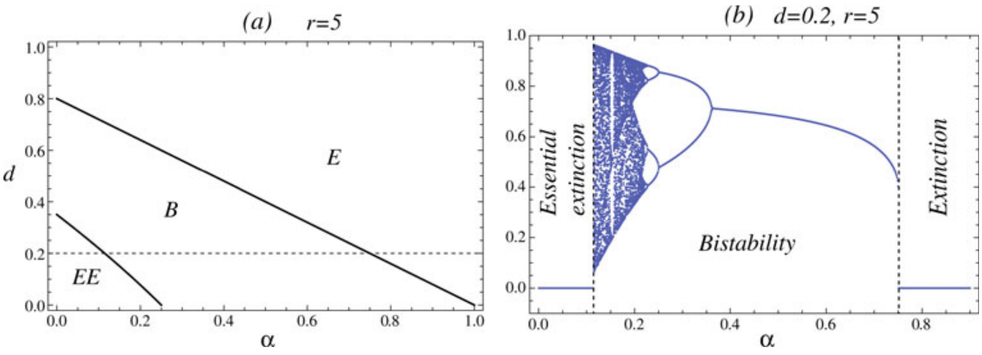

Fig. 2 **a** Bifurcation diagram in the plane of parameters (α, d) for the map $F_{\alpha,d}(x) = \alpha x + (1-\alpha)5x(1-x) - d$; **b** changes in the dynamics of $F_{\alpha,d}$ using α as a bifurcation parameter, for the particular case $d = 0.2$

similar to that of the semelparous population. However, if α is larger ($\alpha > (r-4)/(r-1)$), then the unusual extinction phenomenon is not observed. On the other hand, a new form of this paradox appears: for a given depletion rate that leads the semelparous population to essential extinction, if the probability of adults survivorship increases, then the iteroparous population can persist indefinitely provided that the initial population size has an intermediate value. However, an excessive survivorship rate leads the population to extinction (see Fig. 2b).

The bimodal case: preliminary remarks

Before starting the study of the bimodal case, we comment on some general considerations that will be useful in our discussion.

The first one is that, under conditions A1–A4, the transition between the modes of bistability and extinction always takes place in a saddle-node (or tangent) bifurcation, which occurs when $F_{\alpha,d}$ has exactly two fixed points: 0 and b, with $F'_\alpha(b) = 1$. Since

$$F'_\alpha(b) = 1 \Longleftrightarrow \alpha + (1-\alpha) f'(b) = 1 \Longleftrightarrow f'(b) = 1,$$

$f'(0) > 1$, $f'(c) = 0$, and f' is monotone in $(0, c)$, we conclude that there is a unique $b \in (0, c)$ such that $F'_\alpha(b) = 1$, and b does not depend on α. The tangent bifurcation takes place when $F_{\alpha,d}(b) = F_\alpha(b) - d = b$, that is, for

$$\begin{aligned} d = F_\alpha(b) - b &= \alpha b + (1-\alpha) f(b) - b \\ &= (1-\alpha)(f(b) - b). \end{aligned}$$

Thus, the border between bistability and extinction in the plane of parameters (α, d) is a line with slope $b - f(b) < 0$. Moreover, for values of d sufficiently close to the point of tangent bifurcation, there are three fixed points $0 < K_1 < K_2$, and a simple argument of continuity allows to prove that K_2 is attracting. For a related result, see Gueron (1998, Theorem 1).

The above considerations show that, in the transition from bistability to extinction, the persistent attractor $\mathcal{A}_2$ reduces to a fixed point. In contrast, the jump between essential extinction and bistability always happens in a chaotic regime, by means of a catastrophe bifurcation. For the case $\alpha = 0$, this was proved by Schreiber using the theory of unimodal maps with negative Schwarzian derivative. An alternative point of view, which will be useful in our discussion, is to consider the relation between this type of bifurcation and homoclinic orbits. In Appendix C, we recall the definition of homoclinic orbit and show that existence of this type of orbit is closely related to the boundary collisions that explain the sudden change from bistability to essential extinction. As far as we know, this kind of bifurcation was first described by Grebogi et al. (1982), who called them crises. An interesting remark is that the existence of a homoclinic orbit makes it easier to determine numerically the bifurcation point where a crisis takes place.

The bimodal case: general considerations

Consider the map $F_\alpha(x) = \alpha x + (1-\alpha) f(x)$, where $f : [0, \infty) \to [0, \infty)$ satisfies A1–A4, and $\lim_{x\to\infty} f(x) = 0$. This is the case for such functions as the Ricker and the Bellows maps, among others. From now on, we assume that F_α is bimodal, and denote c_1, c_2 as the points where F_α reaches its local minimum and its local maximum, respectively. In Appendix B, we explain under which conditions F_α is bimodal.

The presence of two critical points, instead of one, has important implications for the population model, and, in particular, regarding the effects of harvesting. The first one is that, as mentioned in the section "The model without harvesting," a population floor is created. Formally, this means that the interval $[F_\alpha(c_2), F_\alpha(c_1)]$ is forward invariant and attracting. As a consequence, for a fixed $\alpha > 0$, there is a value $d_* = d_*(\alpha)$ such that essential extinction is not possible for Eq. 4 if $d \in (0, d_*)$. This is a difference with the quadratic case: in Fig. 2a, we see that essential extinction for $F_{\alpha,d}(x) = \alpha x + (1-\alpha)5x(1-x) - d$ occurs for arbitrarily small values of d if $\alpha \in (0, 0.25)$. Recall that, for $\alpha = 0$, bistability holds if $F_{0,d}$ has three fixed points and $F^2_{0,d}(c) > K_1$ (as usual, we denote by K_1 and K_2 the positive fixed points of $F_{\alpha,d}$, when they exist, with $K_1 < K_2$).

In the bimodal case, this is not necessarily true, because the second critical point enters into the game. Indeed, the first interval of values of d for which there is bistability may lead to essential extinction in a crisis bifurcation when $F_{\alpha,d}(c_2) = K_1$ if $F_{\alpha,d}(c_1) \geq c_2$. We notice that, in this case, the orbit of c_1 is a degenerate homoclinic orbit to the fixed point K_1. However, if $F_{\alpha,d}(c_1) < c_2$ when $F_{\alpha,d}(c_2) = K_1$, then the interval $[F^2_{\alpha,d}(c_1), F_{\alpha,d}(c_1)]$ is forward invariant and bounded away from zero, so there is still bistability until $F^2_{\alpha,d}(c_1) = K_1$.

In Fig. 3, we show the map $F_{\alpha,d}(x) = \max\{\alpha x + (1-\alpha)x\exp(r(1-x)) - d, 0\}$, with $r = 3$, $\alpha = 0.38$, and $d = 0.72$. In this case, $F_{\alpha,d}(c_1) < c_2$ and $F_{\alpha,d}(c_2) < K_1$. Although the second critical point is driven to extinction due to the Allee effect, there is an attracting cycle of period 2 bounded away from zero, which attracts the critical point c_1.

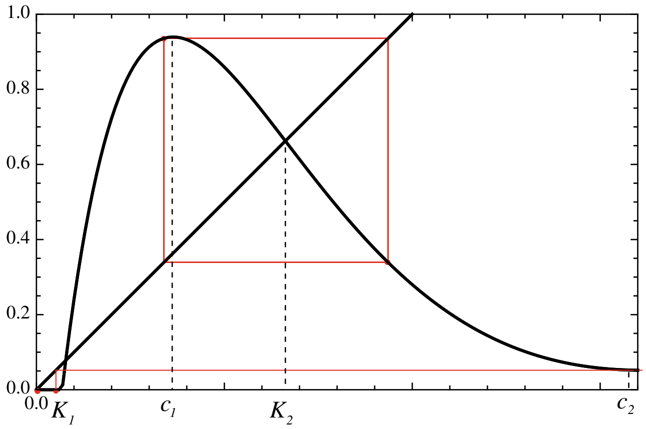

Fig. 3 Orbital diagram showing bistability in the model $x_{n+1} = F_{\alpha,d}(x_n)$, with $F_{\alpha,d}(x) = \max\{\alpha x + (1-\alpha)x\exp(r(1-x)) - d, 0\}$, $r = 3$, $\alpha = 0.38$, and $d = 0.72$

In the rest of the paper, we will present some numerical results obtained for the Ricker model in order to illustrate the effect of harvesting in Eq. 4 in the bimodal case. Our aim is to describe the new modes of survival/extinction, different from those observed in the unimodal case, and to explain the mechanisms that drive the model from one mode to another.

We begin with the case $r = 3$, where it is still possible to reproduce a complete bifurcation diagram in the plane of parameters (d, α). Then, we show that, as r increases, the dynamics of survival and extinction become more and more complex. An important difference is that the relative positions of $F^2_{\alpha,d}(c_1)$ and $F_{\alpha,d}(c_2)$, with respect to the unstable fixed point K_1 arising in the saddle-node bifurcation, are not enough to determine the modes of bistability; the reason is that successive tangent bifurcations occur for the iterates of $F_{\alpha,d}$, and hence, it is necessary to take into account the unstable k-cycles emerging in such bifurcations. As an example, we show some results for the case $r = 5$.

First case of study: the Ricker map with $r = 3$

For small values of the growth rate r in the Ricker model, the influence of the survival rate of adults α and the constant harvesting d can be understood looking at the bifurcation diagram in the plane of parameters (d, α). See Fig. 4, where $F_{\alpha,d}(x) = \max\{\alpha x + (1-\alpha) f(x) - d, 0\}$ is considered with $f(x) = x\exp(3(1-x))$.

We describe the curves plotted in this figure and why they are enough to explain the dynamics of survival/extinction. All curves are obtained numerically. As usual, $0 < K_1 < K_2$ denote the fixed points of $F_{\alpha,d}$, and $c_1 < c_2$ its critical points.

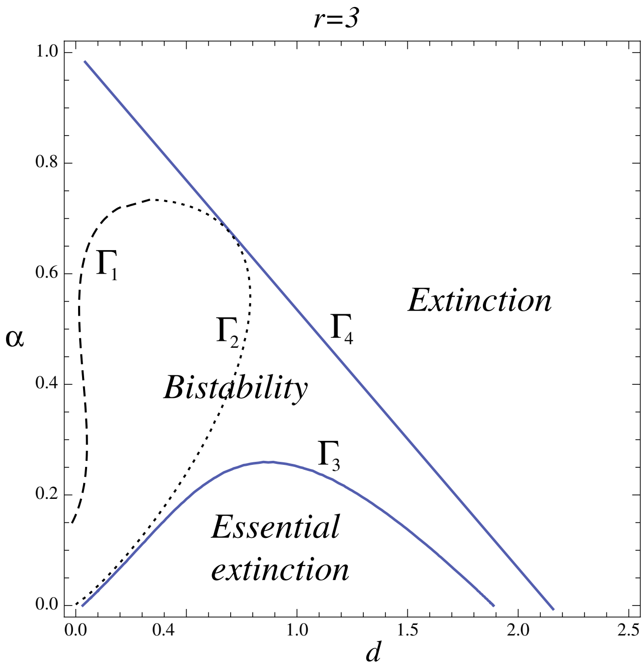

Fig. 4 Bifurcation diagram in the plane of parameters (d, α) for the map $F_{\alpha,d}(x) = \max\{\alpha x + (1-\alpha)x\exp(3(1-x)) - d, 0\}$

- The dashed line Γ_1 on the left of the diagram represents the values (d, α) for which $F_{\alpha,d}(c_1) = c_2$. Thus, $F_{\alpha,d}(c_1) < c_2$ for all values of (α, d) except in the small region placed on the left of Γ_1.
- The dotted line Γ_2 is obtained by solving equation $F_{\alpha,d}(c_2) = K_1$ for d and α.
- The curve Γ_3 corresponds to the solutions of equation $F^2_{\alpha,d}(c_1) = K_1$.
- Finally, the line Γ_4 is the border between bistability and extinction, obtained by the method explained in the section "The bimodal case: preliminary remarks."

Since Γ_1 is on the left of Γ_2 and Γ_3, the transitions between bistability and essential extinction are completely governed by the solutions of equation $F^2_{\alpha,d}(c_1) = K_1$. In the diagram, we can see that this equation has two solutions for α below a critical value $\alpha_* \approx 0.26$, one solution for $\alpha = \alpha_*$, and no solution for $\alpha > \alpha_*$. As a consequence, the unusual dynamics of extinction observed for $\alpha = 0$ holds for small values of α, but not for sufficiently large rates of survivorship. Another consequence of this diagram is that, for a fixed harvesting d, for which essential extinction occurs in the unimodal case $\alpha = 0$, an increasing survival rate leads the system from essential extinction to bistability.

For values of $\alpha > \alpha_*$, only two modes of extinction are possible; one interesting effect of increasing harvesting for these values of α is a period halving forming

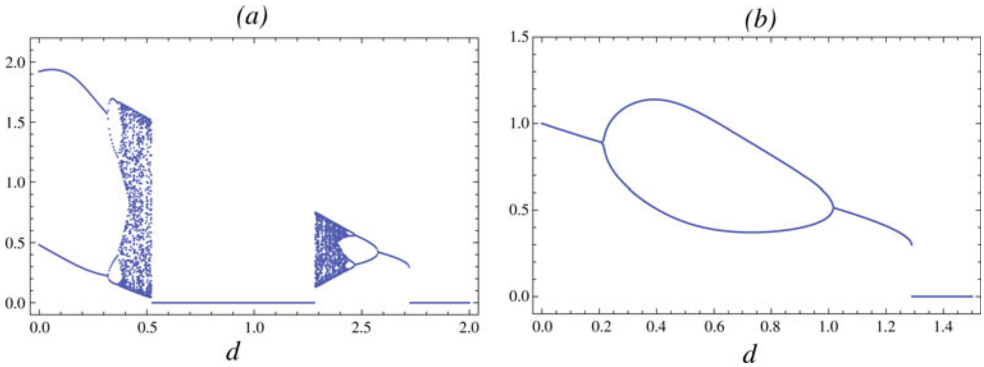

Fig. 5 Bifurcation diagrams for $x_{n+1} = \max\{\alpha x_n + (1 - \alpha) x_n \exp(3(1 - x_n)) - d, 0\}$, using d as a bifurcation parameter with the values **a** $\alpha = 0.2$ and **b** $\alpha = 0.4$

a closed loop-like structure called a primary bubble (Ambika and Sujatha 2000). In Fig. 5, we show the bifurcation diagrams using the parameter d for two fixed values of α, showing the phenomena of unusual extinction ($\alpha = 0.2$), and bubbling ($\alpha = 0.4$).

Some biological consequences can be derived from this analysis. For the generalized Ricker model Eq. 3 with relatively small growth rate, a comment similar to the logistic case holds, that is, the dynamics of extinction of the semelparous population and the iteroparous one are qualitatively similar when the survivorship rate of adults α is small. For larger values of α, two interesting remarks are derived from Figs. 4 and 5: first, the complicated dynamics exhibited by the semelparous model becomes periodic; second, the risk of extinction is prevented if the depletion rate is not too high, since the levels of the population minimum are bounded away from zero (see Fig. 5b). This is due to the fact that the population floor mentioned in the section "The model without harvesting" is big enough to ensure persistence of intermediate population sizes.

Looking at the bifurcation diagram in Fig. 4, we can affirm that determining sustainable levels of harvesting is still possible for a population governed by Eq. 3 if its growth rate r is small. For larger values of r, the situation becomes very different, as shown in the next subsection.

New modes of survival and extinction

The main reason why the diagram in Fig. 4 is relatively simple is that, although F_α has three intervals of monotonicity, the one between c_2 and infinity does not influence the dynamics of extinction because $F_{\alpha,d}(c_1) < c_2$ for all relevant values of α and d.

The situation changes completely as r is increased, because the graph of $F_\alpha(x) = \alpha x + (1 - \alpha) x \exp(r(1 - x))$ is more spiked in the interval $(0, c_2)$, and then $F_{\alpha,d}(c_1)$ is usually larger than c_2. This fact is essential in the emergence of new modes of survival/extinction. In order to explain the mechanism of creation and destruction of these new modes of bistability, we consider the map $F_{\alpha,d}$, where we fix $d = 0.4$, and use r as the bifurcation parameter.

The bifurcation diagram for the unimodal case $\alpha = 0$ is shown in Fig. 6a. There is extinction while the graph of $F_{0,d}$ is below the line $y = x$. A tangent bifurcation takes place at $r = r_1 = 1.15352$, leading to bistability. The attractor bounded away from zero is first the stable fixed point K_1 created in the tangent bifurcation, and then it becomes chaotic after a typical sequence of period-doubling bifurcations. Essential extinction occurs for $r > r_2 = 2.57207$, where a catastrophe bifurcation takes place. Larger values of r cannot reverse this situation, because $F^2_{0,d}(c_1)$ becomes zero for $r > 2.6043$.

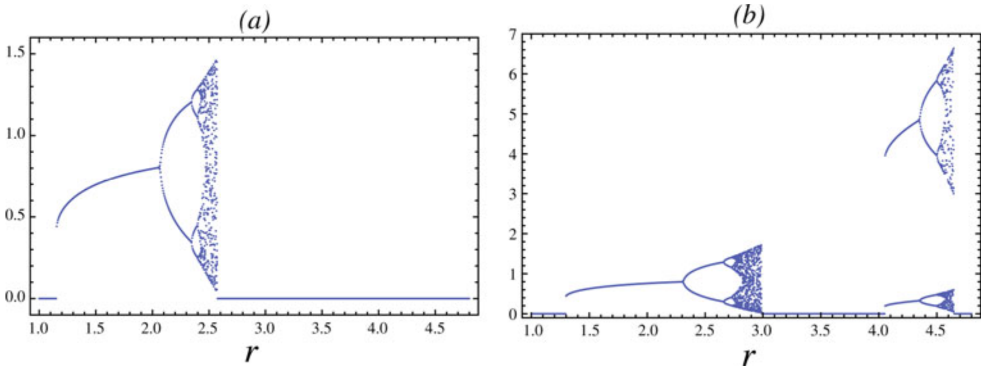

Fig. 6 Bifurcation diagrams for equation $x_{n+1} = \max\{\alpha x_n + (1 - \alpha) x_n \exp(r(1 - x_n)) - 0.4, 0\}$, using r as a bifurcation parameter with the values **a** $\alpha = 0$ and **b** $\alpha = 0.15$

To understand why a new survival mode appears as r is increased in the case $\alpha = 0.15$ (Fig. 6b), we plot a magnification of the bifurcation diagram in Fig. 7. As r reaches the value $r = 4.0509$, a tangent bifurcation for the second iteration $F^2_{\alpha,d}$ occurs, and a couple of cycles of period two are born. One is attracting, and experiences the period doubling cascade to chaos; the other one is repelling, and it is represented in the two dashed curves in Fig. 7. The mechanism of destruction of the chaotic attractor is a crisis that happens when the basin of attraction of the chaotic attractor resulting from the period-doubling sequence collides with the unstable 2-cycle originated in the tangent bifurcation. A similar mechanism was described by Grebogi et al. (1982) for the one-dimensional map $F(x) = C - x^2$, where C is used as bifurcation parameter. In this case, when the collision occurs, a sudden expansion of the attractor takes place. In our example, such an expansion originates essential extinction.

A detailed description of the bifurcation is given in Appendix C. From that study, the bifurcation point at which collision occurs is determined numerically by the formula $F^3_{\alpha,d}(c_1) = F^5_{\alpha,d}(c_1)$, and takes the value $r = 4.6488$. In addition, it is shown that, for a value of r in the regime of bistability ($4.0509 < r < 4.6488$), the set of initial conditions for which the orbit persists indefinitely is not connected. Another consequence of the relation between crises bifurcations and homoclinic points is that catastrophe bifurcations can only happen when the system is in a chaotic regime.

In general, when r is further increased, new intervals of bistability appear in successive tangent bifurcations for the kth iteration of the map $F_{\alpha,d}$. The set of initial conditions for which the orbit persists indefinitely consists of k connected components, and the chaotic attractor is driven to essential extinction in a crisis bifurcation determined by equation $F^{k+1}_{\alpha,d}(c_1) = F^{2k+1}_{\alpha,d}(c_1)$. In particular, for the value of r at which the crisis occurs, there is a degenerate homoclinic orbit from the critical point c_1 to the unstable k-cycle that arises in the tangent bifurcation.

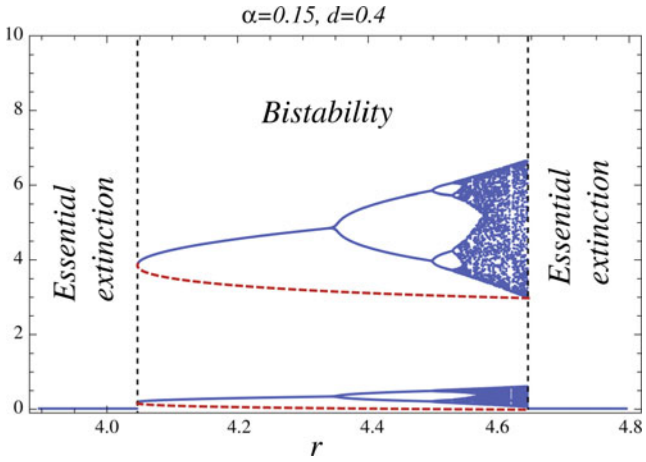

Fig. 7 Magnification of the bifurcation diagram for equation $x_{n+1} = \max\{0.15x_n + (1 - 0.15)x_n \exp(r(1 - x_n)) - 0.4, 0\}$, using r as a bifurcation parameter

In our example, a tangent bifurcation for $F^3_{\alpha,d}$ occurs at $r = 6.30241$, and the crisis bifurcation leading again to essential extinction takes place for $r = 6.63927$.

Second case of study: the Ricker map with $r = 5$

To illustrate how the new modes of bistability appear when the harvesting rate is increased, we consider the Ricker map $f(x) = x\exp(5(1 - x))$ with a survivorship rate $\alpha = 0.15$. As usual, we denote $F_\alpha(x) = \alpha x + (1 - \alpha) f(x)$, and $F_{\alpha,d}(x) = \max\{F_\alpha(x) - d, 0\}$.

We will show that, as d is increased, there are several regions of essential extinction alternating with regions of bistability. This is a clear difference with the unimodal case ($\alpha = 0$), where only an interval of essential extinction is possible.

The critical points of F_α are $c_1 = 0.200649$ and $c_2 = 1.7574$, with $F_\alpha(c_1) = 9.31173$, $F_\alpha(c_2) = 0.297464$. The interval $[F_\alpha(c_2), F_\alpha(c_1)]$ is forward invariant and attracting for the map F_α, and, as a consequence, there is bistability for $F_{\alpha,d}$ if d is small enough.

The first crisis bifurcation leading to essential extinction takes place at $d_1 = 0.295081$, where $F_{\alpha,d_1}(c_2) = K_1$. Thus, the orbit of c_2 is homoclinic to the first positive fixed point K_1 of $F_{\alpha,d}$. A new mode of bistability is born at $d_2 = 0.901469$, where a second crisis bifurcation occurs. The value of d_2 is found solving equation $F^3_{\alpha,d}(c_1) = F^5_{\alpha,d}(c_1)$, that is, the orbit of c_1 is homoclinic to a 2-cycle of $F_{\alpha,d}$.

A new transition from bistability to essential extinction takes place in a tangent bifurcation for $F^2_{\alpha,d}$ at $d_3 = 1.05162$. This point is calculated solving numerically the system of equations $(F^2_{\alpha,d})'(x) = 1$, $F^2_{\alpha,d}(x) = x$.

The diagram showing the bifurcation points d_1, d_2, and d_3 is plotted in Fig. 8a.

For $d > d_3$, there is a quite long interval of essential extinction, but there is still another interval of bistability prior to extinction. This interval is always present due to the arguments discussed in the subsection "The bimodal case: preliminary remarks." The point $d_4 = 9.09319$, marking the transition from essential extinction to bistability, is found by solving equation $F^2_{\alpha,d}(c_1) = F^3_{\alpha,d}(c_1)$, that is, a new crisis bifurcation occurs when $F^2_{\alpha,d}(c_1) = K_1$. The tangent bifurcation leading from bistability to extinction takes place at

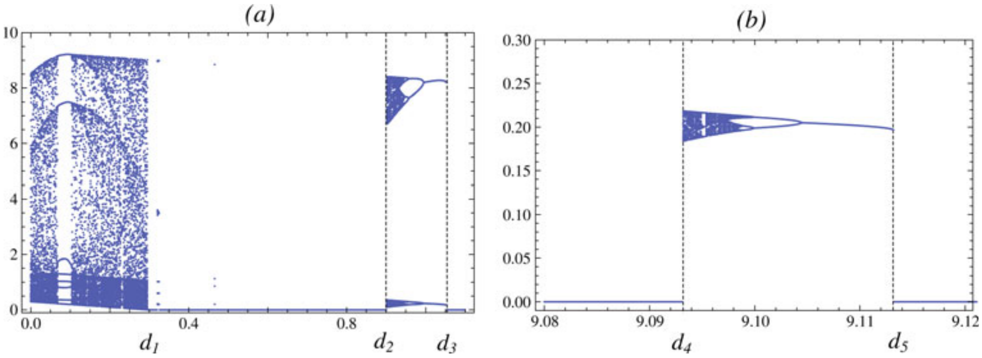

Fig. 8 Bifurcation diagrams for $x_{n+1} = \max\{0.15x_n + (1 - 0.15)x_n \exp(5(1 - x_n)) - d, 0\}$, using d as a bifurcation parameter. The ranges of values are **a** $d \in [0, 1.1]$ and **b** $d \in [9.08, 9.12]$

$d_5 = F_\alpha(b) - b = 9.11322$, where $b = 0.196402$ is the unique solution of equation $f'(b) = 1$. The diagram showing the bifurcation points d_4 and d_5 is plotted in Fig. 8b.

If we look more closely at Fig. 8a, we can observe some "shadows" in the interval of essential extinction, close to d_1. Actually, the magnification of the bifurcation diagram shown in Fig. 9 reveals that there is a small range of parameters between 0.32 and 0.326 for which there is bistability. We call this interval a "window" of bistability. These windows are created and destroyed by the mechanisms described in Appendix C. In this case, numerically solving equation $F^6_{\alpha,d}(c_1) = F^{11}_{\alpha,d}(c_1)$, we get the value $d = 0.320667$ at which the orbit of c_1 is homoclinic to a periodic orbit of $F_{\alpha,d}$ of period five. The solution of the system $(F^5_{\alpha,d})'(x) = 1$, $F^5_{\alpha,d}(x) = x$ provides the value $d = 0.325085$ at which a tangent bifurcation for $F^5_{\alpha,d}$ occurs, leading the system again from bistability to essential extinction.

This example shows the complexity that models governed by bimodal maps and subject to harvesting can exhibit. Moreover, we can conclude that two-parameter bifurcation diagrams similar to those in Figs. 2a and 4 are, in general, very difficult to construct.

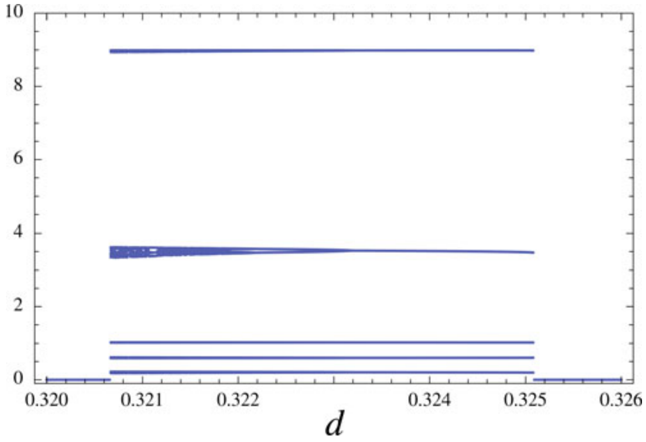

Fig. 9 Magnification of the bifurcation diagram in the interval $d \in [0.32, 0.326]$ for equation $x_{n+1} = \max\{0.15x_n + (1 - 0.15)x_n \exp(5(1 - x_n)) - d, 0\}$. A period five window of bistability is observed

Discussion

For semelparous populations with nonoverlapping generations and overcompensating density dependence, a typical model is a recurrence $x_{n+1} = f(x_n)$, where x_n is the size of the population at time n, and f is a unimodal map. Assuming that these populations are subject to constant harvesting in every period of time, it was proved that continuous changes in the amount of captures can lead the population to essential extinction abruptly. This phenomenon was explained by means of bifurcations of catastrophe type or crises, due to boundary collisions (Vandermeer and Yodzis 1999; Schreiber 2001). Schreiber demonstrated that essential extinction occurs when the maximum size of a growing population exceeds a critical population density.

Apart from these abrupt changes, counterintuitive effects have been described in the study of population models subject to different strategies of harvesting. Perhaps the most famous is the paradoxical enrichment effect in the stock size of a population when mortality is increased. This phenomenon is called the hydra effect, and a good reference is the recent survey of Abrams (2009). It is linked to discrete models with proportional harvesting, that is, when a percentage of the population stock is removed each year (Seno 2008; Liz 2009). As it is reported by Abrams, the possibility of this paradoxical effect was first suggested by Ricker in his famous paper (Ricker 1954). A similar effect was found in the studies of control by simple limiters, that is, the population stock is prevented from reaching values over a fixed threshold (Hilker and Westerhoff 2006).

Even more surprising is the paradoxical effect of unusual extinction, discovered by Sinha and Parthasarathy and later confirmed by Schreiber. The interesting observation of Sinha and Parthasarathy is that increasing harvesting not only can give place to a sudden essential extinction, but also the population may change unexpectedly from a regime of essential extinction to one of bistability, in which the population stock persists indefinitely for a large set of initial conditions (the expression "large set" means here that it contains a nontrivial real interval).

In this paper, we studied the effect of harvesting in a population model characterized by the fact that generations overlap because a certain fraction of adults survive from time period to time period, while juveniles experience overcompensating density dependence. The consideration of a survival rate has two important consequences in the model. On the one hand, it helps to stabilize the system; on the other hand, it makes the population less susceptible to extinction because a floor is created below which the population cannot fall. For some known functions, such as the Ricker and the Bellows maps, this floor is due to a new critical point that converts the unimodal profile of f into a hump-with-tail (or bimodal) function $F_\alpha(x) = \alpha x + (1-\alpha) f(x)$. Other mechanisms to create population floors in one-dimensional discrete ecological models are the consideration of a constant amount of immigration (McCallum 1992; Stone 1993; Sinha and Das 1997; Stone and Hart 1999), or the application of a limiter control from below (Hilker and Westerhoff 2005). For more discussions, see, e.g., Ruxton and Rohani (1998).

However, the new critical point that aids population persistence also induces more complexity in the dynamics of the population growth. The main differences in the behavior of survival and extinction in the iteroparous model, compared with the semelparous one, are motivated by its bimodal shape. Actually, adding a survivorship term to the quadratic map does not originate a new critical point, and for this reason, the behavior of this model is relatively simple.

We point out the fundamental differences found in our study:

- In general, an arbitrary small value of the harvesting parameter d can drive to extinction a population without adult survivorship under a strong overcompensating density dependence. In contrast, for a bimodal model, the mentioned population floor ensures persistence for a set of initial conditions when d is small enough.
- While in a model of population growth governed by a unimodal map, increasing the growth rate r leads the system to essential extinction; in the bimodal case, larger values of r may result in new modes of bistability. The crises bifurcations responsible of this complex behavior are more intricate, and they cannot be explained only by the relative position between the positive equilibria of the system and the forward iterations of the critical points. Moreover, in these new modes of bistability, the population stock can be placed in several disjoint chaotic bands bounded away from zero, alternating from one band to another in successive time periods.
- As a consequence, the unusual extinction phenomenon—in which persistence is possible even if there is essential extinction for lower depletion rates—becomes more complex in the bimodal case. Indeed, there may be several intervals of bistability alternating with intervals of essential extinction when the harvesting parameter is increased.

Although these studies might be applicable to resource management policies in fisheries, we share the words of caution common in all papers devoted to studying the complex behavior in the population growth due to harvesting. Even if theoretical research suggests that sometimes increasing captures may help either to avoid extinction or to increase the stock size of the population, this fact should not be used to justify greater harvesting. Rather, our study highlights the difficulty in determining sustainable harvesting rates for iteroparous populations experiencing overcompensating density dependence.

To finish, our contribution can be seen as a first step in the study of the influence of harvesting in the delayed Clark's model (Clark 1976)

$$x_{n+1} = \alpha x_n + (1-\alpha) f(x_{n-T}),$$

where the integer $T \geq 1$ represents a maturation delay. For example, the age of sexual maturity is estimated at $T = 5$ years for the Greenland–Spitzberger Bowhead and other northern whale species (Conrad 1989; Allen and Keay 2004).

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Appendix A

This appendix is devoted to give more details on the derivation of Eq. 2 from ecological models for the

Ricker and the logistic maps. An interesting derivation of Eq. 2, with f being the Ricker map, is given in the book of Thieme (2003). Taking into account the survivorship assumption, the resulting difference equation is

$$y_{n+1} = y_n \left(q + \gamma e^{-y_n}\right), \tag{6}$$

where $q \in [0, 1]$ is an adult's probability of surviving 1 year including the reproductive season, and γ is the number of per capita offspring still alive after 1 year if there is no cannibalism (we refer to Thieme (2003, Section 9.2) for more details).

If $q + \gamma > 1$, then there is a unique positive equilibrium K of Eq. 6. Notice that this provides a dependence relation among the parameters q, K, and γ, namely,

$$1 = q + \gamma e^{-K}. \tag{7}$$

This relation is sometimes referred to as *the balance equation* (May 1980).

Replacing Eq. 7 into Eq. 6 leads to

$$y_{n+1} = y_n \left(q + (1-q)e^{K-y_n}\right) = qy_n + (1-q)y_n e^{K-y_n}.$$

Setting $y_n = Kx_n$, $r = K$, $q = \alpha$, the positive equilibrium is normalized to 1, and Eq. 6, reads

$$x_{n+1} = \alpha x_n + (1-\alpha)x_n e^{r(1-x_n)}.$$

Using similar arguments, May (1980) (see also Fisher 1984) derived equation

$$y_{n+1} = \alpha y_n + (1-\alpha)y_n \left(1 + q\left(1 - \frac{y_n}{K}\right)\right)^z, \tag{8}$$

used by the International Whaling Commission (IWC) (Beddington 1978; Beddington and May 1980) to describe the dynamical behavior of baleen whale populations. The meaning of the parameters in Eq. 8 is the following: K is the positive equilibrium, q is the maximum increase in fecundity of which population is capable at low densities, and z measures the severity with which the density-dependent response is manifested. The case $z = 1$ corresponds to the logistic assumption, in which the density-dependent increase in fecundity is linear. After normalization, Eq. 8 with $z = 1$ is rewritten as

$$x_{n+1} = \alpha x_n + (1-\alpha)rx_n(1-x_n),$$

with $r = 1 + q$, $qy_n = (1+q)Kx_n$.

Appendix B

Assume that f satisfies A1–A4, and $\lim_{x\to\infty} f(x) = 0$. Since $f'(c) = 0$, $f'(x) < 0$ for all $x > c$, and $\lim_{x\to\infty} f(x) = 0$, it follows that f has an inflexion point at $f(\delta)$, for some $\delta > c$. Moreover, this is the unique inflexion point of f. Indeed, condition A3 ensures that f has, at most, one inflexion point on each interval not containing a critical point (this is a consequence of Lemma 3 in Schreiber 2001). On the other hand, condition A4 prevents the existence of inflexion points on $[0, c]$. Therefore, it is clear that $f'(\delta) = \min\{f'(x) : x > 0\}$.

Consider $F_\alpha(x) = \alpha x + (1-\alpha)f(x)$, with $\alpha \in (0, 1)$. Since $F'_\alpha(x) = 0 \Longleftrightarrow f'(x) = -\alpha/(1-\alpha)$, we distinguish two cases:

(a) *Monotone case.* If $f'(\delta) \geq -\alpha/(1-\alpha)$, then

$$F'_\alpha(x) = \alpha + (1-\alpha)f'(x) \geq \alpha + (1-\alpha)f'(\delta) \geq 0, \ \forall x > 0.$$

Hence, F_α is nondecreasing on $(0, \infty)$, and therefore, there are only two possible modes of survival/extinction for Eq. 4:

- Extinction: if 0 is the unique fixed point of $F_{\alpha,d}$, then $\lim_{n\to\infty} F^n_{\alpha,d}(x) = 0$ for all $x > 0$.
- Bistability: if there are $0 < K_1 \leq K_2$ such that $F_{\alpha,d}(K_1) = K_1$, $F_{\alpha,d}(K_2) = K_2$, then $\lim_{n\to\infty} F^n_{\alpha,d}(x) = 0$ for all $x \in (0, K_1)$ and $\lim_{n\to\infty} F^n_{\alpha,d}(x) = K_2$ for all $x > K_1$.

(b) *Bimodal case.* If $f'(\delta) < -\alpha/(1-\alpha)$, then equation $F'_\alpha(x) = 0$ has two solutions c_1, c_2, with $0 < c_1 < \delta < c_2$. Moreover, $F'_\alpha(x) > 0$ on $(0, c_1) \cup (c_2, \infty)$, and $F'_\alpha(x) < 0$ on (c_1, c_2). This means that $F_\alpha(c_1)$ is a local maximum, and $F_\alpha(c_2)$ is a local minimum.

For example, for the Ricker map $f(x) = x\exp(r(1-x))$, the inflexion point is reached at $\delta = 2/r$, and the minimum of f' is $f'(\delta) = -\exp(r-2)$. Thus, $F_\alpha(x) = \alpha x + (1-\alpha)x\exp(r(1-x))$ is bimodal for all $r > 2 + \ln(\alpha/(1-\alpha))$.

Appendix C

We recall (Block and Coppel 1992, Section III.3) that, if g is a continuous map from a real interval I into itself, a point y is homoclinic to a periodic point z of period $k \geq 1$ if $f^{k\cdot n}(y) = z$ for some $n > 0$, and y belongs to the unstable manifold of z. As proved in (Proposition 21, p. 64, of the same book), a continuous map is chaotic if and only if it has a homoclinic point.

It is clear that the condition for chaotic semi-stability in Theorem 1 of Schreiber (2001) is equivalent to saying that the critical point c is homoclinic to the least positive fixed point of f. The orbit formed by the homoclinic point, its preimages, and its (finite) forward orbit is a homoclinic orbit. Moreover, if this orbit contains a critical point, it is called a degenerate homoclinic orbit (Devaney 1989, Section 1.16). See Fig. 10, where a degenerate homoclinic orbit is represented.

For α and d fixed, consider the map $F_{\alpha,d}(x) = \max\{\alpha x + (1-\alpha)x\exp(r(1-x)) - d, 0\}$ used in the paper as a paradigm of the influence of harvesting in a population model governed by a bimodal map.

For $\alpha = 0$, the catastrophe bifurcation (Fig. 6a) occurs when the basin of attraction of the chaotic attractor collides with the unstable fixed point arising in the tangent bifurcation, that is, when $F^2_{0,d}(c_1) = K_1$. At this bifurcation point, the orbit of c_1 is homoclinic to K_1, as shown in Fig. 10.

For $\alpha > 0$, there are more modes of survival and extinction. They are typically created, as r is increased, in tangent bifurcations for an iterate $F^k_{\alpha,d}$, $k \geq 1$, and destroyed when the basin of attraction of the chaotic attractor created by a period doubling cascade from the stable k-cycle collides with the unstable k-cycle originated in the tangent bifurcation. When $k = 1$, this simply means that $F^2_{\alpha,d}(c_1) = K_1$. For $k > 1$, there is a degenerate homoclinic orbit to the unstable k-cycle. In particular, this remark provides the formula $F^{k+1}_{\alpha,d}(c_1) = F^{2k+1}_{\alpha,d}(c_1)$, which is useful to numerically determine the bifurcation point.

To explain how the survival mode is destroyed in a crisis bifurcation, let us look at the example given in the section "New modes of survival and extinction," that is, $F_{\alpha,d}(x) = \max\{0.15x + (1-0.15)x\exp(r(1-x)) - 0.4, 0\}$. As indicated in the section "New modes of survival and extinction," a transition from essential extinction to bistability takes place as the parameter r is increased, via a tangent bifurcation for the second iteration $F^2_{\alpha,d}$.

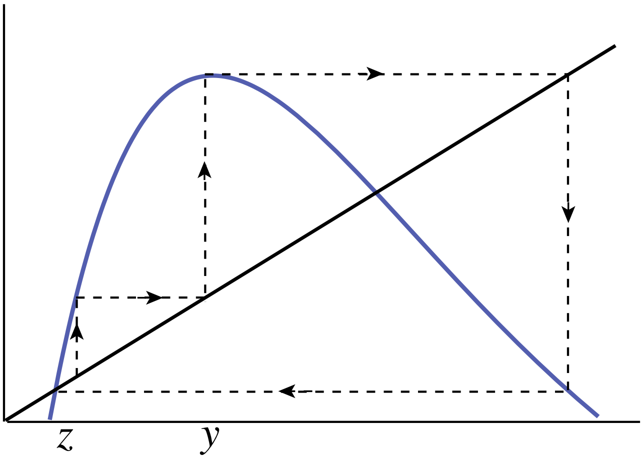

Fig. 10 A degenerate homoclinic orbit to a fixed point z. For the critical point y, $g^2(y) = z$, and the preimages $g^{-n}(y)$ converge to z as $n \to \infty$

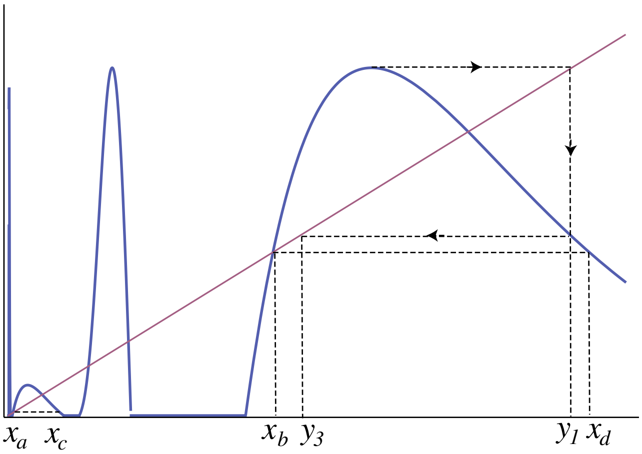

Fig. 11 Graphic representation of the map $F^2_{\alpha,d} = F_{\alpha,d} \circ F_{\alpha,d}$, where $F_{\alpha,d}(x) = \max\{0.15x + (1-0.15)x\exp(r(1-x)) - 0.4, 0\}$ with $r = 4.6$

It is useful to use a graphic representation of $F^2_{\alpha,d}$. In Fig. 11, this is made for the value $r = 4.6$, belonging to the region of bistability. After the tangent bifurcation, two 2-cycles arise. The unstable 2-cycle $\{x_a, x_b\}$ gives two fixed points of $F^2_{\alpha,d}$. Now, we can determine two points x_c, x_d, such that

$$x_c = \min\left\{x > x_a \; : \; F^2_{\alpha,d}(x) = x_a\right\} \; ;$$

$$x_d = \min\left\{x > x_b \; : \; F^2_{\alpha,d}(x) = x_b\right\} .$$

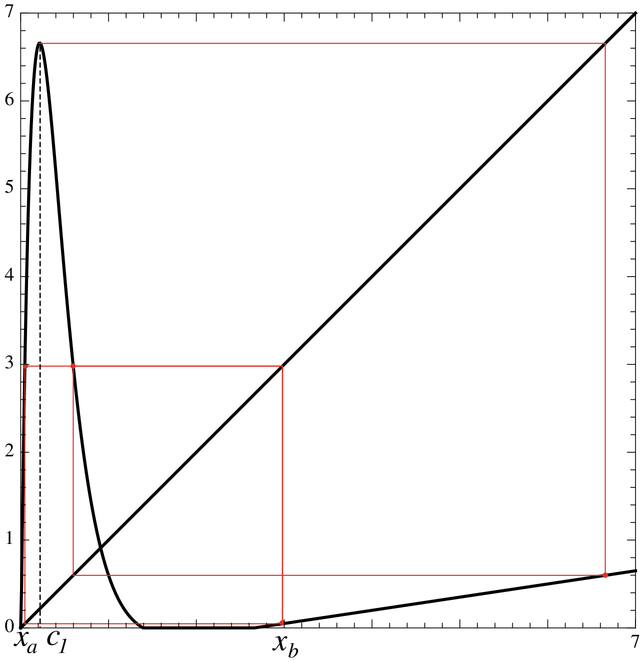

Fig. 12 Graphic of the map $F_{\alpha,d}(x) = \max\{0.15x + (1-0.15)x\exp(r(1-x)) - 0.4, 0\}$ with $r = 4.6488$. There is a homoclinic orbit to the 2-cycle $\{x_a, x_b\}$

Denote $I_1 = [x_a, x_c]$ and $I_2 = [x_b, x_d]$. It is clear that $F_{\alpha,d}(I_1) = I_2$ and $F_{\alpha,d}(I_2) = I_1$. Moreover, the set of initial conditions for which the orbit persists indefinitely is $I_1 \cup I_2$. The crisis bifurcation occurs when $y_1 := F_{\alpha,d}(c_1) = x_d$, that is, when $y_3 := F^3_{\alpha,d}(c_1) = x_b$. Notice that this relation defines the homoclinic orbit from c_1 to the cycle of period two. Moreover, since $F^2_{\alpha,d}(x_b) = x_b$, we get the formula $F^3_{\alpha,d}(c_1) = F^5_{\alpha,d}(c_1)$, from which the bifurcation value $r = 4.6488$ is determined numerically. In Fig. 12, we represent the map $F_{\alpha,d}$ with $r = 4.6488$, for which $F^3_{\alpha,d}(c_1) = x_b$, giving place to a degenerate homoclinic orbit.

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