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Proportional threshold harvesting in discrete-time population models

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Abstract

Threshold-based harvesting strategies tend to give high yields while protecting the exploited population. A significant drawback, however, is the possibility of harvesting moratoria with their socio-economic consequences, if the population size falls below the threshold and harvesting is not allowed anymore. Proportional threshold harvesting (PTH) is a strategy, where only a fraction of the population surplus above the threshold is harvested. It has been suggested to overcome the drawbacks of threshold-based strategies. Here, we use discrete-time single-species models and rigorously analyze the impact of PTH on population dynamics and stability. We find that the population response to PTH can be markedly different depending on the specific population model. Reducing the threshold and allowing more harvest can be destabilizing (for the Ricker and Hassell map), stabilizing (for the quadratic map), or both (for the generalized Beverton–Holt map). Similarly, management actions in the form of increasing the threshold do not always improve population stability—this can also be due to bistability. Our results therefore emphasize the importance of a rigorous analysis in investigating the impact of PTH on population stability.

Keywords Harvesting strategy · Population dynamics · Stability · Population cycles · Maximum sustainable yield · Harvesting frequency

Mathematics Subject Classification 92D25 · 39A10 · 39A30 · 39A60

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1 Introduction

Sustainable harvesting has to balance at least two demands that seemingly conflict each other, namely to protect biological resources on the one hand and to produce large yields on the other hand. Harvesting strategies adjust the target harvest from year-to-year based on the population size and potentially other economic, social, or environmental conditions. The most common and simplest harvesting strategies specify the target harvest as a function of the population size only (Getz and Haight 1989; Hilborn and Walters 1992; Punt 2010). Examples include constant-yield harvesting, proportional harvesting, and threshold harvesting (e.g. Lande et al 2001; Sinclair et al 2006).

Proportional threshold harvesting (PTH) is a strategy, where a constant proportion of the surplus of the population above a set threshold is harvested. If the population is below the threshold, no harvesting takes place—which allows the resource to recover at the highest natural rate when being below the threshold. Proportional threshold harvesting has been used to manage U.S. west coast pelagic species (Pacific Fishery Management Council 1998), and it has been suggested for the management of brown bears in Norway (Tufto et al 1999), wolverines in Scandinavia (Sæther et al 2005), and Eurasian lynx in Norway (Sæther et al 2010). It has also been considered as a harvesting strategy for Pacific whiting (Ishimura et al 2005) and Norwegian spring-spawning herring (Conrad et al 1998; Kaitala et al 2003; Enberg 2005; Lillegård et al 2005).

The term 'proportional threshold harvesting' seems to go back to Engen et al (1997). They proposed this strategy when there is high uncertainty in population estimates. The same strategy emerged in simulations by Clark and Kirkwood (1986). Even more generally, PTH arises whenever the harvest is a linear function of the population size and the vertical intercept is negative (Hilborn and Walters 1992, pp 456), an assumption often made by regulators and resource managers (Homans and Wilen 1997; Conrad et al 1998). Furthermore, PTH can be seen as a special case of the "40–10" rule, which is used to manage U.S. west coast groundfish (see Deroba and Bence 2008, and references therein).

PTH includes two well-known harvesting strategies as special cases. First, we obtain threshold harvesting (TH) when the entire surplus of the population above the threshold is harvested. This strategy is usually characterized by high average yields and reasonable stock protection but also by high variability in yield. Second, we obtain proportional harvesting (PH) when the threshold is zero. This strategy is usually characterized by lower average yields and higher extinction riks but also by lower variability in yield. It thus appears that high yields and safe population levels almost always appear to come at the cost of high variability in yield (Ricker 1958; Gatto and Rinaldi 1976; Reed 1979; Hall et al 1988; Quinn II et al 1990; Lande et al 1995, 1997).

PTH seems to unite attractive features from both threshold harvesting in form of high yields and safe populations and from proportional harvesting in form of little variability in yield (Engen et al 1997; Lande et al 2003; Enberg 2005). The reduced variability in yield is due to less harvest moratoria, which are enforced when the population falls below the threshold. Temporary fisheries closures can be a major economic problem including social and political issues (Hilborn and Walters 1992;

Steele et al 1992), which is why PTH may overcome some of the biggest drawbacks of threshold-based harvest policies. Moroever, PTH tends to allow for lower threshold values so that the population can fluctuate over a wider range of densities. This is beneficial for a more robust and adaptive population assessment (Walters 1986). PTH also seems to be rather robust against observation errors (Engen et al 1997) as well as parameter uncertainties (Fieberg 2004). Lande et al (1997) have therefore argued that objections against threshold-based harvesting strategies in the case of PTH lose much of their force.

Surprisingly, simulation studies of the Norwegian spring-spawning herring fishery, which is characterized by heavy fluctuations caused by positively autocorrelated environmental stochasticity, exhibit mixed results. In an unstructured model, Kaitala et al (2003) could not find the expected superiority of PTH, as none of the considered strategies (PH, TH, PTH) performed significantly better than the other. By contrast, using age-structured simulation models, Enberg (2005) and Lillegård et al (2005) found that PTH performed best among these strategies. A general evaluation of harvesting strategies is difficult, as their performance depends on the evaluation criteria used, errors in population estimates, uncertainties in policy parameters, and the type of environmental fluctuations (Milner-Gulland et al 2001; Deroba and Bence 2008). The current theory on PTH relies to a large degree on diffusion models, assuming that any change in population size is small and ignoring delay effects. Fluctuations are assumed to be caused by external forces, thus excluding endogeneously generated cycles or chaos (Engen et al 1997; Lande et al 1997). Yet, both causes of population oscillations have profound implications for the optimal management of populations (Hudson and Dobson 2001; Kokko 2001; Sæther et al 2001; Barraquand et al 2017).

Hence, there remain gaps for rigorous mathematical results on PTH in populations that can change markedly from one generation to the next one (e.g., as is typical for overcompensation) and especially for population cycles that emerge inherently due to time lags, nonlinearities, or species interactions. Here, we study PTH in a number of discrete-time single species models that can exhibit regular or irregular oscillations due to overcompensation. Our focus will be on how harvesting affects the dynamic stability, and how this impacts population size, yield, variability of yield, and the possibility of multistability.

2 The model

We begin by describing population growth in the absence of harvesting and then include proportional threshold harvesting. By passing, we will point out the differences of this harvesting strategy compared to proportional harvesting (also called constant-effort harvesting) and threshold harvesting (also called fixed escapement).

Let $x_n \geq 0$ be the population density at time step n, $n = 0, 1, 2 \ldots$. In the absence of harvesting, we assume that population growth can be described by the difference equation

$$x_{n+1} = f(x_n), \tag{2.1}$$

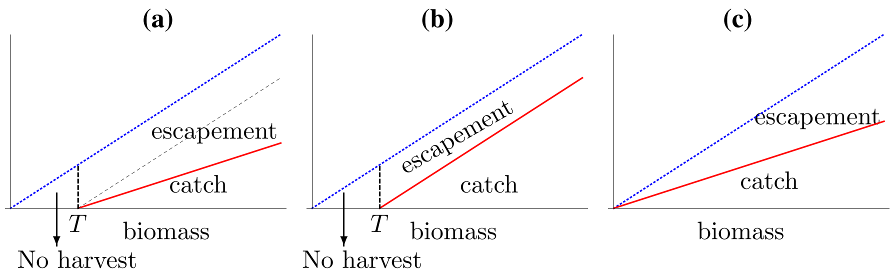

Fig. 1 Different harvesting strategies illustrated by sketching catch or harvest mortality (red solid lines) as a function of population density or biomass. **a** proportional threshold harvesting; **b** threshold harvesting; **c** proportional harvesting. The blue dotted lines indicate the identity diagonal line. T is the threshold value, and the harvest proportion q corresponds to the slope of the red lines (color figure online)

and an initial value $x_0 > 0$. The map f is the production (or stock–recruitment curve), for which we assume typical conditions for single-species population models:

(A) $f : [0, \infty) \to [0, \infty)$ is continuous, has a unique positive fixed point K, $f(x) > x$ for $x \in (0, K)$, and $0 < f(x) < x$ for $x > K$.

Under threshold harvesting, the population dynamics is described by the difference equation

$$x_{n+1} = \min\{f(x_n), T\} := g_T(x_n) = \begin{cases} f(x_n) & \text{if } f(x_n) \le T, \\ T & \text{if } f(x_n) > T, \end{cases} \tag{2.2}$$

where $T > 0$ is the threshold. That is, all excess individuals of the population above the threshold are harvested so that only a population density equal to the threshold escapes the harvest and remains. If the population density (after reproduction) is below the threshold, no harvesting takes place.

With proportional threshold harvesting, only a fraction $q(f(x) - T)$ of the surplus above the threshold is harvested, where $q \in (0, 1]$ is the (asymptotic) harvest proportion. The mathematical model is given by

$$x_{n+1} = F(x_n) := \begin{cases} f(x_n) & \text{if } f(x_n) \le T, \\ f(x_n) - q(f(x_n) - T) & \text{if } f(x_n) > T. \end{cases} \tag{2.3}$$

The map $F(x)$ can be written as

$$F(x) = F_{q,T}(x) := \min\{f(x), (1-q)f(x) + qT\}$$

and depends on the two harvesting parameters q and T. In order to avoid complicated notation, we only refer to this dependence if it is needed. For example, for a fixed threshold value T, we sometimes refer to F as F_q to emphasize its dependence on the harvest proportion q.

The model with threshold harvesting (2.2) is a particular case of (2.3) for $q = 1$, that is $g_T = F_{1,T}$. It is worth noticing that (2.3) also contains proportional harvesting as a particular case when $T = 0$. See Fig. 1 for an illustration.

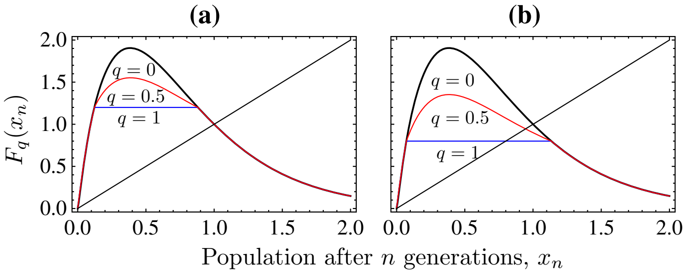

Fig. 2 Diagrams showing the map F_q for a Ricker function $f(x) = x\,e^{2.6(1-x)}$ and different harvest proportions q: no harvest for $q = 0$, threshold harvesting for $q = 1$, and half of the surplus is harvested when $q = 0.5$. **a** $T = 1.2 > K$, **b** $T = 0.8 < K$

Equation (2.3) has been considered in the literature under different names. For example, Stoop and Wagner (2003) call it *softer limiter control*, while they refer to the case $q = 1$ as *hard limiter control*. Franco and Perán (2013) call (2.3) *target-oriented threshold control*, since the harvesting strategy can be seen as a combination of threshold harvesting and target-oriented control (Dattani et al 2011; Franco and Liz 2013).

3 Stability results

In this section we study harvesting-induced stability switches. With stability switch, we refer to a change in the local asymptotic stability of the nontrivial equilibrium. We will focus on the case of lowering the threshold T, thus increasing harvesting pressure, but we will also investigate the impact of increasing the harvesting proportion q, which also increases harvesting pressure.

For convenience, we introduce the following hypothesis:

(H) $f : [0, \infty) \to [0, \infty)$ is a twice differentiable map satisfying assumption **(A)**, and there exists $d > 0$ (d can be ∞) such that $f'(x) > 0$ in $(0, d)$, and $f'(x) < 0$ in (d, K) (if $d < K$). Moreover, $f''(x) < 0$ for all $x \in (0, d)$.

Assumption **(H)** is satisfied by usual compensatory models (e.g., Beverton–Holt) and overcompensatory models such as the Ricker model, the generalized Beverton–Holt model (Maynard Smith and Slatkin model), and the Hassell model. For the Beverton–Holt model, $d = \infty$ in **(H)**. We can also consider examples such as the quadratic map, where $f : [0, A] \to [0, A]$, $0 < A < \infty$, and the rest of the conditions hold.

We distinguish two cases, depending on the relative size of the threshold T and the nontrivial equilibrium K of the unharvested population.

- Case I: $T > K$. In this case, the map $f(x)$ without harvesting and the map $F(x)$ with harvesting share the same positive equilibrium K (see Fig. 2a). Since $F'(K) = f'(K)$, the local asymptotic stability of the equilibrium does not depend on the parameters q and T. Moreover, if K is a global attractor for (2.1) in the absence of harvesting, then K is also a global attractor of (2.3) in the presence of PTH, for all $q \in (0, 1]$ and $T \geq K$ (see Proposition A.3 in "Appendix A.4").

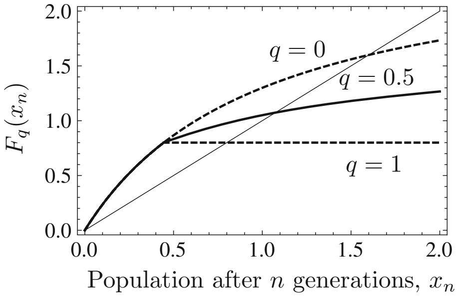

Fig. 3 Diagram showing the map F_q for a Beverton–Holt function $f(x) = 2.6x/(1 + x)$, $T = 0.8$, and different values of q: no harvest for $q = 0$, threshold harvesting for $q = 1$, and half of the surplus is harvested when $q = 0.5$

- Case II: $T < K$. In this case, under hypothesis **(H)**, model F_q with PTH has a unique positive fixed point $K_1 = K_1(q, T)$ for each $q \in (0, 1)$, and $K_1 \in (T, K)$ (see Proposition A.1 in "Appendix A.1"). It can be checked that the equilibrium $K_1(q, T)$ is a decreasing function of q for each fixed value of $T < K$, and it is an increasing function of T for every fixed value of $q \in (0, 1)$ (see Franco and Liz 2013 and Fig. 2b). Moreover, for a fixed value of $T \in [0, 1)$, increasing q is stabilizing (Franco and Liz 2013, Theorem 1). By *stabilizing* we mean that an unstable equilibrium becomes locally stable for sufficiently large values of q.

If $F'(K_1) \geq 0$, i.e. population dynamics at equilibrium does not show overcompensation, then K_1 is globally asymptotically stable (see "Appendix A.2"). This is the case, for example, in the Beverton–Holt model (see Fig. 3), but also for overcompensatory population models when the equilibrium is on the increasing branch of the map and shows local undercompensation.

If $T = K$, then increasing q cannot destabilize a stable positive equilibrium, but it can stabilize it, as we will show later.

Therefore, in the following we assume that $T \leq K$ and $F'(K_1) < 0$. In this case, the existence of stability switches as the threshold T is varied is directly related to changes in the derivative of the map f at the positive equilibrium $K_1 = K_1(q, T)$ of F. A related discussion can be found in Doebeli (1995) who studied the potentially stabilizing effects of immigration of a constant number of individuals into a population (see also Stone and Hart 1999 for further discussions).

For simplicity, we assume that the positive fixed point of f is $K = 1$, which can always be achieved by a simple change of variables $y = x/K$.

We will now consider different population growth models. We will find that lowering the threshold T can

(i) stabilize the equilibrium when f is concave on $(0, 1)$ like in the quadratic model;
(ii) destabilize the equilibrium when f is hump-shaped and has an inflection point on the decreasing branch like in the Ricker and Hassell model; and
(iii) both stabilize and destabilize the equilibrium when f is as flexible as in the generalized Beverton–Holt or Maynard Smith and Slatkin model.

3.1 Quadratic model

If f is concave on $(0, 1)$, then Proposition A.2 in "Appendix A.3" ensures that decreasing T cannot destabilize the equilibrium.

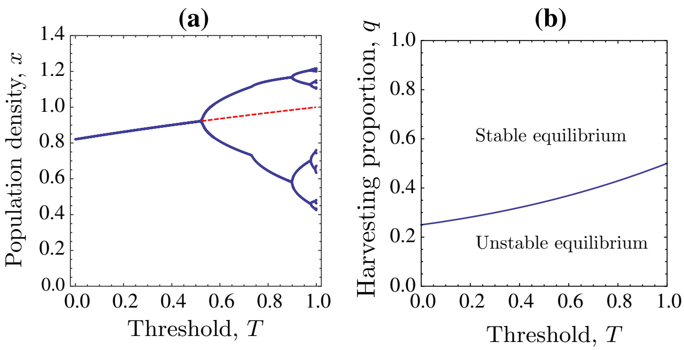

Fig. 4 **a** Bifurcation diagram of the PTH model (2.3) for the quadratic map with $r = 4$ and $q = 0.35$, showing a situation when decreasing T is stabilizing. The red dashed line corresponds to the unstable fixed point. **b** Stability diagram of (2.3) in the parameter plane (T, q) for the quadratic map with $r = 4$ (color figure online)

A simple example of a concave function is provided by the quadratic map, which, after normalization, reads

$$f(x) = x\,(r - (r-1)x)\,, \quad r > 1, \quad 0 \le x \le r/(r-1). \tag{3.1}$$

It is well known that the positive equilibrium $K = 1$ of f is globally asymptotically stable if $1 < r \le 3$ and unstable if $r > 3$. In the latter case, a stability switch as T is decreased (stabilizing the equilibrium K_1) occurs for all q that satisfy

$$\frac{r-3}{r} < q < \frac{r-3}{r-2}$$

(see Proposition A.8 in "Appendix A.6").

A particular example with $r = 4$ and $q = 0.35 \in (0.25, 0.5)$ is shown in Fig. 4a. Here, the stability switch correponds to a supercritical period-doubling bifurcation. Its location in the two-parameter plane (T, q) is shown in Fig. 4b and defines the boundary of the stability region.

3.2 Ricker model

In contrast with the previous example, many population maps are not concave in the whole interval (0, 1). Instead, there is an inflection point $z < 1$, which changes the potential population responses with respect to stability when the threshold T is decreased. This is the case for the Ricker and the Hassell model. Here, we focus on the Ricker map, which reads in normalized form

$$f(x) = x\,\mathrm{e}^{r(1-x)}, \quad r > 0. \tag{3.2}$$

The positive equilibrium $K = 1$ of f is globally asymptotically stable if $r \le 2$ and unstable if $r > 2$. There is a unique inflection point $z = 2/r$, which is obviously less

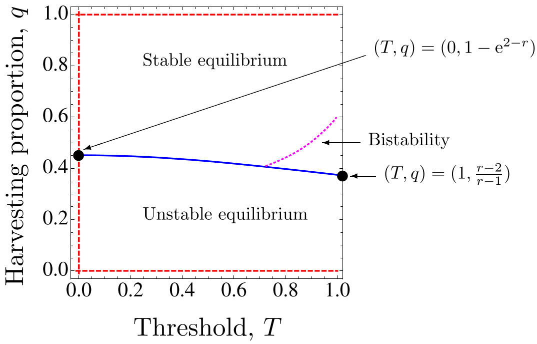

Fig. 5 Stability diagram of the PTH model (2.3) for the Ricker map $f(x) = x\,e^{r(1-x)}$, with $r = 2.6$. Dashed red lines correspond to the limit cases $q = 0$ (original map (2.1) without any harvesting), $q = 1$ (TH), and $T = 0$ (PH) (color figure online)

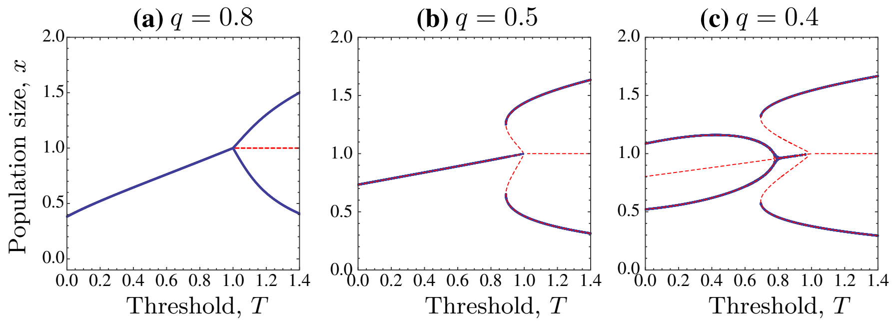

Fig. 6 Bifurcation diagrams for (2.3) with $f(x) = x\,e^{r(1-x)}$, $r = 2.6$, and different values of q. Red dashed lines correspond to unstable fixed points and unstable 2-periodic orbits. For more details, see the main text (color figure online)

than 1 if $r > 2$. In "Appendix A.5" we prove that a stability switch as T is decreased can only occur if $r > 2$ and

$$\frac{r-2}{r-1} < q < 1 - e^{2-r}. \tag{3.3}$$

Moreover, for fixed values of r and q satisfying (3.3), decreasing T destabilizes the positive equilibrium K_1 of F. Figure 5 shows the stability diagram of the PTH model (2.3) for the Ricker map with $r = 2.6$. Note that in the limit case of threshold harvesting ($q = 1$) the equilibrium is always globally asymptotically stable if $T \leq K$ (see Lemma 2 in "Appendix A.2").

Figure 6 shows a selection of different bifurcation diagrams with varying threshold T, each for a different value of the harvesting proportion q.

- For a harvesting proportion $q = 0.8$ (Fig. 6a), the equilibrium K_1 is asymptotically stable for all $T < 1$. As the threshold crosses the critical point $T = 1$, which is the scaled carrying capacity, the equilibrium undergoes a supercritical flip bifurcation. We notice that the bifurcation is not smooth, in the sense that the local stability of the equilibrium changes abruptly from $F'(1) < -1$ for $T > 1$ to $F'(1) > -1$ for $T < 1$.

- For a harvesting proportion $q = 0.5$ (Fig. 6b), the equilibrium K_1 is also asymptotically stable for all $T < 1$, but it undergoes a *subcritical* flip bifurcation as the threshold crosses the critical point $T = 1$. As a consequence, there is bistability: for values of T close to 1, the stable equilibrium K_1 coexists with an attracting 2-periodic orbit.
- For a harvesting proportion $q = 0.4$ (Fig. 6c), the equilibrium K_1 is destabilized in a supercritical flip bifurcation at a threshold value below $T = 1$. In addition, the subcritical flip bifurcation at $T = 1$ still persists. For some values of T, bistability is observed either between K_1 and a 2-periodic attractor, or between two 2-periodic attractors. Note that the supercritical flip bifurcation at $T < 1$, when $F'(K_1) = -1$, occurs smoothly in this case.

As a consequence of the previous results for the Ricker model, we observe that a more protective strategy (choosing larger values of the threshold T) tends to stabilize the population for intermediate harvesting proportions q (Fig. 6c). However, setting the threshold above the carrying capacity $K = 1$ may destabilize the population again. Moreover, the stabilized equilibrium may coexist with another attractor, so that sufficiently large perturbations could shift the population to a periodic cycle rather than a fixed point. If we consider the Hassell map, the dynamic behavior of the PTH model (2.3) is very similar to the one we have described for the Ricker map. Indeed, for the normalized Hassell model

$$x_{n+1} = \frac{x_n(1+b)^m}{(1+bx_n)^m}, \quad b > 0,\ m > 1,$$

the positive equilibrium $K = 1$ is globally asymptotically stable if $mb \le 2(1+b)$ (Liz 2007) and unstable if $mb > 2(1+b)$. In the latter case, the unique inflection point $z = 2/(b(m+1))$ is less than 1.

3.3 Generalized Beverton–Holt model

The previous examples show that decreasing the threshold T below the carrying capacity can have either stabilizing (quadratic map) or destabilizing effects (e.g., Ricker and Hassell map) on the positive equilibrium of a population subject to PTH. In this subsection we show that actually two stability switches can occur as T decreases from $T = 1$ to $T = 0$. We consider the population map proposed by Maynard Smith and Slatkin (1973), which generalizes the Beverton–Holt model as follows:

$$f(x) = \frac{ax}{1+(a-1)x^m}, \quad a > 1, \quad m > 1. \tag{3.4}$$

The equilibrium $K = 1$ of f is globally asymptotically stable if either $m \le 2$, or $m > 2$ and $a \le m/(m-2)$, and it is unstable if $m > 2$ and $a > m/(m-2)$. Stability switches for decreasing thresholds T can only occur in the latter case. We next show that the flexibility provided by the two parameters in the model allows for different scenarios.

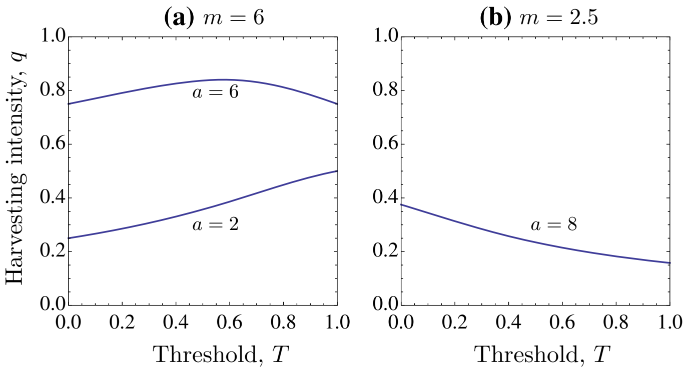

Fig. 7 Stability diagram of the PTH model (2.3) for a generalized Beverton–Holt map given by (3.4), with **a** $m = 6$, **b** $m = 2.5$, and different values of a. In each case, the equilibrium is stable above the stability boundary and unstable below it

It can be checked that the map f defined in (3.4) is concave in (0, 1) if and only if $f''(1) \leq 0$, which is equivalent to the condition $a \leq 2m/(m-1)$. In this case, the situation is similar to that of the quadratic map: decreasing the threshold T can have a stabilizing effect. An example is shown in Fig. 7a for $m = 6$ and $a = 2 < 12/5$, and in Fig. 8a.

The unique positive equilibrium K_1 of the PTH model (2.3) with f defined by (3.4) is locally asymptotically stable if and only if $(1-q)f'(K_1) \geq -1$. In the limit cases $T = 0$ and $T = 1$, simple calculations allow us to obtain an analytic local stability condition in terms of a, m, and q:

- For $T = 0$ (PH), K_1 is asymptotically stable if and only if

$$q \geq 1 - \frac{m}{(m-2)a} =: q_1(a).$$

- For $T = 1$ (TH), it is clear that $K_1 = 1$, and the limit form of the stability condition for K_1 is given by the inequality $(1-q)f'(1) > -1$, which is equivalent to

$$q > \frac{(m-2)a - m}{(m-1)a - m} =: q_2(a).$$

In the previous examples, the corresponding values of q_1 and q_2 satisfy the monotonicity conditions $q_1 < q_2$ (for the quadratic map) or $q_1 > q_2$ (for the Ricker map). For the generalized Beverton–Holt map (3.4), all cases are possible. Actually, $q_1(a) < q_2(a)$ if and only if $a < m$. If we choose $a = m > 3$, then $q_1(a) = q_2(a) = (m-3)/(m-2)$, and we easily find examples with two stability switches as T is decreased. The case $a = m = 6$ is shown in Figs. 7 and 8b. If $2 < m < 3 < a$, then $q_1(a) > q_2(a)$, and we observe a population stability response to decreasing T similar to the one displayed by the Ricker model; for example, the case $m = 2.5$ and $a = 8$ is shown in Figs. 7 and 8c.

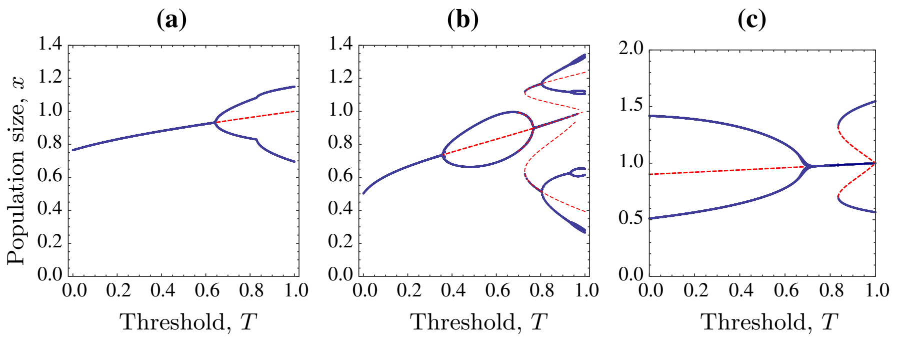

Fig. 8 Bifurcation diagrams for the PTH model (2.3) with the generalized Beverton–Holt map $f(x) = ax/(1+(a-1)x^m)$, using T as the bifurcation parameter. Red dashed lines correspond to unstable fixed points and unstable 2-periodic points. **a** Decreasing T is stabilizing for $a=2$, $m=6$, and $q=0.4$. **b** There are two stability switches for $a=6$, $m=6$, and $q=0.82$. **c** Decreasing T is destabilizing for $a=8$, $m=2.5$, and $q=0.2$ (color figure online)

Table 1 Summary of results

	K asymptotically stable	K unstable
$T > K$	K_1 asymptotically stable	K_1 unstable
$T \leq K, q = 1$	K_1 asymptotically stable	K_1 asymptotically stable
$T \leq K, q < 1$	K_1 asymptotically stable	Increasing q is stabilizing; decreasing T can stabilize, destabilize, or produce two stability switches (Subsects. 3.1, 3.2, and 3.3)
$T = 0$[a]	K_1 asymptotically stable	Increasing q is stabilizing

[a]Liz (2010)

T is the threshold, q is the harvesting proportion, K is the positive equilibrium (carrying capacity) of the unharvested population, and K_1 is the equilibrium of the harvested population. The limit cases $q=1$ and $T=0$ correspond to threshold harvesting and proportional harvesting, respectively

Table 1 provides a summary of the results for the PTH strategy (2.3) with compensatory and overcompensatory models satisfying some mild assumptions considered in this paper. It also includes results for the special cases of proportional harvesting and threshold harvesting for comparison.

4 Maximum yield and harvest frequency

With proportional threshold harvesting, the yield obtained in generation n is given by

$$Y_n = \begin{cases} 0 & \text{if } f(x_n) \leq T, \\ q(f(x_n) - T) & \text{if } f(x_n) > T. \end{cases}$$

If assumption **(A)** holds, $T < K$, and the equilibrium K_1 of the PTH model (2.3) is a global attractor, then the asymptotic value for the yield is $Y = q(f(K_1) - T)$. Since, by definition, $K_1 = F(K_1) = (1-q)f(K_1) + qT$, we can write the asymptotic yield as

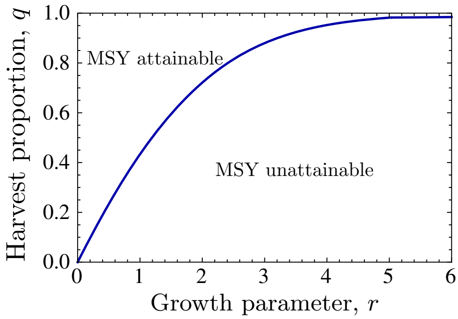

Fig. 9 The maximum sustainable yield (MSY) is attainable for populations with small growth parameters and for large harvest proportions. PTH model (2.3) with the Ricker map $f(x) = x\,\mathrm{e}^{r(1-x)}$. The curve shown is r^* from (4.2)

$$Y = q(f(K_1) - T) = f(K_1) - K_1.$$

Thus, the maximum sustainable yield (MSY) is attained when the equilibrium K_1 maximizes the function $f(x) - x$, that is, when $f'(K_1) = 1$ (assuming f is continuously differentiable). In particular, for given values of r and q, the MSY can be only attained if the system

$$f'(x) = 1, \quad (1-q)f(x) + qT = x \tag{4.1}$$

has a solution (x, T) with $x > 0$, $T \in (0, K)$.

For the normalized Ricker map $f(x) = x\,\mathrm{e}^{r(1-x)}$, we have $K = 1$, and the MSY can be attained if and only if

$$r < q - \ln(1-q) := r^* \tag{4.2}$$

(see Proposition A.9 in "Appendix A.7"). Notice that in the limit case $q = 1$ (TH), condition (4.2) always holds, and therefore the MSY can be attained for all populations with any value of r. For PTH with $q < 1$ and $r > r^*$, however, the MSY cannot be attained. That is, in fast growing populations and for large harvest proportions, the threshold T cannot be chosen optimally in the sense of maximizing the yield. According to condition (4.2), the higher the growth parameter, the larger the harvest proportion required to attain the MSY (see also Fig. 9). If the MSY is not attainable, the highest yield will be obtained by choosing the boundary condition $T = 0$, which corresponds to PH (see below for examples).

If the population is oscillatory, then additional local maxima for the yield can appear, for threshold values above the carrying capacity.

In the general case, it is difficult to carry out a rigorous theoretical analysis of the yield. Some phenomena as bistability, the lack of smoothness of the return map F, and the different bifurcations observed as T is varied have a strong influence on the behavior of the yield depending on the model parameters.

In the following, we illustrate our discussion with some examples of the PTH model (2.3) with the normalized Ricker map $f(x) = x\,\mathrm{e}^{r(1-x)}$.

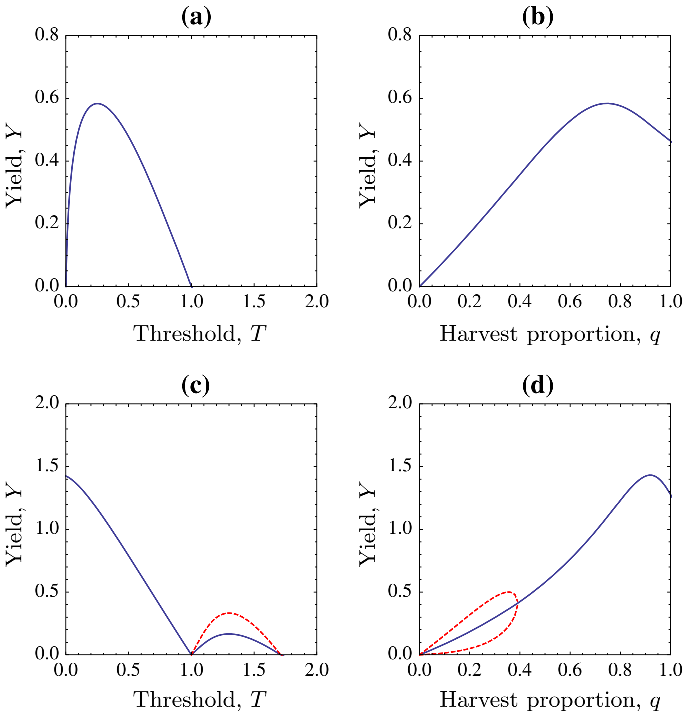

Fig. 10 Asymptotic values (blue solid lines) of the yield for (2.3) with the Ricker map $f(x) = x\,\mathrm{e}^{r(1-x)}$. In the top row, $r = 1.5$ for which the positive equilibrium is a global attractor; in the bottom row, $r = 2.5$ which allows for instabilities. **a** We fix $q = 0.8$ and plot the yield as the threshold T is increased from $T = 0$ to $T = 1$. In this case, $r < r^* = 0.8 - \ln(0.2) \approx 2.40944$, so the MSY is attained at a positive value of T. **b** We fix $T = 0.2$ and plot the yield as q is increased from $q = 0$ to $q = 1$. **c** We fix $q = 0.8$. Since $r = 2.5 > r^*$, the MSY is attained at the limit case $T = 0$. For $T > 1$, the positive equilibrium is unstable and the red dashed line indicates the yield when intervention occurs, but it takes place only every other year. **d** For $T = 0.2$, a flip bifurcation occurs as q passes the critical value $q^* \approx 0.3905$. The red dashed lines correspond to the yield at odd and even years when the population is oscillatory ($q < q^*$). In this case, harvesting occurs every year (color figure online)

First we choose $q = 0.8$, so that $r^* = 0.8 - \ln(0.2) \approx 2.40944$.

- For $r = 1.5 < r^*$, the equilibrium K_1 under PTH (2.3) is always a global attractor for $T \in [0, 1)$ (see Proposition A.4 in "Appendix A.4"). Moreover, for $T \geq 1$, the equilibrium is $K_1 = 1$, and therefore $f(K_1) = 1 \leq T$, which implies that there is no yield. For $T < 1$, the MSY is attained at $T \approx 0.251$, for which system (4.1) has a solution $x \approx 0.397$, giving a yield $Y_{\max} \approx 0.58386$. See Fig. 10a.
- For $r = 2.5 > r^*$, the MSY is not attained at any positive threshold value T, and the yield is a decreasing function of T for $T \in (0, 1)$. For $T > 1$, there is a 2-periodic attractor, and a new local maximum for the yield is attained. We emphasize that the periodic attractor $\{p_1, p_2\}$ satisfies $f(p_1) > T > f(p_2)$, and therefore harvest occurs only once every two years. This means that the asymptotic value for the average annual harvest is $\bar{Y} = q(f(p_1) - T)/2$. See Fig. 10c.

Next, for a fixed value of r, the MSY condition (4.2) is fulfilled for q close enough to 1. Thus, if the positive equilibrium under PTH (2.3) is a global attractor, the MSY can be always attained for a suitable value of q.

- For the stable case $r = 1.5$ and $T = 0.2$, the MSY is attained for $q \approx 0.7478$, with an approximate value of $Y_{\max} \approx 0.5838$. This case is represented in Fig. 10b.
- For $r = 2.5$ and $T = 0.2$, the positive equilibrium is unstable for $0 < q < q^* \approx 0.3905$ and asymptotically stable if $q^* < q < 1$. Our simulations indicate that the equilibrium is globally attracting in the latter case, and there is a 2-periodic cycle attracting all nontrivial positive solutions if $0 < q < q^*$. Moreover, if we denote the 2-cycle by $\{p_1, p_2\}$, we get the inequalities $T < f(p_2) < f(p_1)$. This means that, contrary to what happens in the case $q = 0.8$ discussed above, harvest occurs every year. See Fig. 10d, where we plot the average yield depending on the harvest proportion.

5 Discussion and conclusions

Proportional threshold harvesting has been considered as the optimal harvesting strategy among proportional harvesting and threshold harvesting in terms of yield, maximum yield, population level and risk, and the variability of risk (e.g. Engen et al 1997; Lande et al 1997; Enberg 2005). Here, we have investigated the impact of PTH on the stability of population dynamics and on yield and harvesting frequencies. Increasing harvesting pressure, by reducing the threshold, can have a stabilizing effect (in the case of the quadratic map), a destabilizing effect (in the case of the Ricker and Hassell maps), or both (in the case of the generalized Beverton–Holt map).

In general, existing theory considers increased harvesting pressure to have a destabilizing impact on populations with externally generated fluctuations (Beddington and May 1977; May et al 1978). When population fluctuations are internally generated, as is the case considered here, current theory considers harvesting to have a stabilizing effect (Milner-Gulland and Mace 1998; Jonzén et al 2003). In this paper we have shown for the first time that harvesting can destabilize equilibria in models as simple as the Ricker or Hassell map, i.e., in populations with overcompensation. So far, this was only known for models that additionally included iteropacy (Liz 2010; Liz and Pilarczyk 2012; Liz and Ruiz-Herrera 2012; Cid et al 2014; Liz and Hilker 2014), carry-over effects (Liz and Ruiz-Herrera 2016), or seasonal density dependence (Liz 2017).

In PTH, there are two ways to increase harvesting mortality, namely by reducing the threshold or by increasing the harvesting proportion. We have found that the latter case always has a stabilizing effect. Hence, it clearly matters for stability how and at which population densities harvesting pressure is varied. Establishing thresholds is thought to be a precautionary measure, preventing risk of overexploitation and promoting persistence (FAO 1995; Ludwig 1998; Quinn II and Deriso 1999; ICES 2011). The destabilizing effect of increasing the threshold, as observed for the quadratic map and in some parameter ranges of the generalized Beverton–Holt map, is therefore particularly concerning. Similarly, in the case of the Ricker map, increasing the threshold can move the population from a stable equilibrium to the bistability region (see Fig. 5). In the bistable region, the population can be destabilized by strong enough perturbations. Again, an increased threshold does not necessarily promote stability.

For the results in this paper, we provide full analytic proofs for the Ricker map and the quadratic maps in the Appendix. The results for the other population maps are also rigorous, although we do not provide analytic proofs; for the Hassel map the proofs are similar to the ones for the Ricker map; and for the generalized Beverton–Holt map we only need examples and analytic proofs would be hard to write.

All population models considered in this paper, except for the Beverton–Holt model, are unimodal. These models are often assumed to behave similarly. Yet, the dynamic responses to increased harvesting are very different. This paper therefore suggests some interesting differences between the population models. We speculate that the different responses may be related to the inflection point of the decreasing branch of the population map. If it doesn't exist like in concave models, we found increased PTH to be stabilizing; if the location of the inflection point is below the unharvested carrying capacity, we found increased PTH to be destabilizing. Note that both the Hassell and the generalized Beverton–Holt map are two-parametric functions, but the inflection point of the unstable Hassell map is always below the unharvested carrying capacity, while the generalized Beverton–Holt model is more flexible and can show both a stabilizing and destabilizing response to increases in PTH.

We have also observed a number of differences between harvesting strategies. In particular, for TH (when $q = 1$) the destabilizing effect of increased harvesting pressure (by lowering the threshold) is impossible for the Ricker map; the equilibrium of the Ricker model under threshold harvesting has been shown to be always globally asymptotically stable if $T \leq K$.

Another major difference is that under TH the MSY can always be attained for the Ricker map. By contrast, this is not the case for PTH. For a given harvest proportion, the MSY cannot be attained if the population growth parameter is larger than a critical value (see Fig. 9). This critical value increases with the harvest proportion. In populations with a small growth parameter, the MSY can only be attained if the harvest proportion q is small. In populations with a large growth parameter, however, it requires a larger harvest proportion to be able to attain the MSY, so maximizing the yield becomes more difficult for fast growing populations. For a given threshold, the harvest proportion can always be chosen to obtain the MSY.

When populations oscillate in the absence of harvesting, they may overshoot the carrying capacity. This allows for additional local maxima in the yield for thresholds above the carrying capacity (see Fig. 10c). As a consequence, however, there will be generations in which the population density drops below the threshold and harvesting will not be allowed, thus reducing harvest frequency. In PTH, we observed another interesting phenomenon. For threshold values below the carrying capacity, the population can fluctuate but its densities remain above the threshold. Hence, there will be oscillations with a high variability in yield, but the harvest frequency remains 1 (see Fig. 10d).

We didn't consider stochasticity, so harvest moratoria occur only when $T > K$ and dynamics are unstable. For moratoria to occur when $T < K$, we need to consider the effect of stochasticity. Moreover, we didn't consider age structure or any other form of structure. Results of Enberg (2005) suggest that considering age structure may be important as the conclusions changed in comparison to Kaitala et al (2003), but since both models relied on different assumptions and on simulations only, it is unclear whether the differences are only due to age structure. This underlines the benefit of rigorous results obtained from a mathematical analysis.

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A Appendix

A.1 Existence and uniqueness of a positive equilibrium of (2.3)

We first prove a technical lemma.

Lemma 1 *Let* $g : [a, b] \to \mathbb{R}$ *be a twice differentiable map such that* $g'(x) > 0$ *and* $g''(x) < 0$ *for all* $x \in (a, b)$*, and* $g(a) > a$*. Then* g *can have at most one fixed point* p *in* $(a, b]$*. Moreover, the fixed point exists if and only if* $g(b) \le b$*.*

Proof Assume that the set of fixed points of g is not empty, and denote by p_1 the infimum of this set. Since $g(a) > a$, it is clear that $g'(p_1) \le 1$. By the hypotheses, $g'(x) < 1$ for all $x > p_1$. This excludes the possibility of more fixed points of g, and implies that $g(b) \le b$. Bolzano's Theorem ensures the existence of a fixed point of g when $g(a) > a$ and $g(b) \le b$. □

Proposition A.1 *Assume that* f *satisifies* **(H)** *and* $T < K$*. Then* F_q *has a unique positive fixed point* $K_1 = K_1(q, T) \in (T, K)$ *for each* $q \in (0, 1)$*.*

Proof We first prove the uniqueness of the fixed point of F_q, dividing the proof into two steps.

Step 1: F_q *cannot have positive fixed points in* $(0, T] \cup [K, \infty)$.

For a fixed $q \in (0, 1)$, F_q is a convex combination of $f(x)$ and $F_1(x)$. Actually, $F_q(x) = (1 - q)f(x) + cF_1(x)$, for all $x \ge 0$. Hence,

$$\left.\begin{array}{ll} f(x) \le x, & \forall x \ge K \\ F_1(x) < x, & \forall x \ge K \end{array}\right\} \Longrightarrow F_q(x) < x, \quad \forall x \ge K,$$

$$\left.\begin{array}{ll} f(x) > x, & \forall x \le T \\ F_1(x) \ge x, & \forall x \le T \end{array}\right\} \Longrightarrow F_q(x) > x, \quad \forall x \le T.$$

Step 2: F_q *has a unique positive fixed point* $K_1 \in (T, K)$.

We notice that $F_q(x) = (1-q)f(x) + qT$ for all $x \in (T, K)$, and therefore $F_q'(x)$ and $F_q''(x)$ have the same sign as $f'(x)$ and $f''(x)$, respectively.

If $d \ge K$, then $F_q'(x) > 0$ and $F_q''(x) < 0$ for all $x \in (T, K)$. Since $F_q(T) > T$ and $F_q(K) < K$, Lemma 1 ensures that F_q has a unique fixed point $K_1 \in (T, K)$.

In the following, we assume that $d < K$ and consider two cases.

Case 1: $F_q(d) < d$.

In this case, F_q cannot have fixed points in (d, K). By Lemma 1, $F_q(T) > T$ and $F_q(d) < d$ imply that F_q has a unique fixed point $K_1 \in (T, d) \subset (T, K)$.

Case 2: $F_q(d) \geq d$.

In this case, Lemma 1 guarantees that F_q cannot have any fixed point in (T, d). Since $F_q'(x) < 0$ for all $x \in (d, K)$, $F_q(d) \geq d$, and $F_q(K) < K$, it follows from Bolzano's and Rolle's theorems that there exists a unique $K_1 \in [d, K) \subset (T, K)$ such that $F_q(K_1) = K_1$. □

A.2 Global stability for (2.3) when $F'(K_1) \geq 0$

If the map f satisfies **(H)** and F is nondecreasing at the positive equilibrium K_1, then K_1 attracts all solutions of (2.3) starting at a positive initial condition. This result is a direct consequence of Proposition A.1 and the following auxiliary result:

Lemma 2 (Braverman and Liz 2012, Lemma 1) *Let $g : [0, \infty) \to [0, \infty)$ be a continuous function such that $g(0) = 0$, and g has a unique fixed point p such that $x < g(x) \leq p$ for all $x \in (0, p)$, and $0 < g(x) < x$ for all $x > p$. Then p is globally attracting for all positive solutions of the equation*

$$x_{n+1} = g(x_n), \tag{A.1}$$

that is, every solution $\{x_n\}$ of (A.1) with $x_0 > 0$ converges to p.

A.3 Local stability for (2.3) when f is concave in $(0, K)$

Proposition A.2 *Assume that f satisfies* **(H)**, *and $f''(x) < 0$ for all $x \in (0, K)$. If K is asymptotically stable for (2.1), then the unique positive equilibrium $K_1 = K_1(q, T)$ of (2.3) is asymptotically stable for all $q \in (0, 1)$ and $T < K$. Moreover, if K_1 is asymptotically stable for given values of $q \in (0, 1)$ and $T \in (0, K)$, then decreasing T cannot destabilize the equilibrium.*

Proof Assume first that K is asymptotically stable for (2.1). Since $f''(x) < 0$ for all $x \in (T, K)$, $K_1 < K$, and $|f'(K)| \leq 1$, it follows that

$$|F_q'(K_1)| = (1 - q)|f'(K_1)| \leq (1 - q)|f'(K)| < 1.$$

This implies that K_1 is asymptotically stable.

If $K_1(q, T_1)$ is asymptotically stable for given values of $q \in (0, 1)$ and $T_1 \in (0, K)$, then the same argument used above applies to prove that $K_1(q, T_2)$ is asymptotically stable if $T_2 < T_1$. We only need to use that $T_2 < T_1$ implies $T < K_1(q, T_2) < K_1(q, T_1) < K$ (see Franco and Liz 2013). □

A.4 Global stability for (2.3) with a stable Ricker map

In this section we prove that if the positive equilibrium $K = 1$ of the Ricker map (3.2) is globally asymptotically stable, then the same property holds for all $q \in (0, 1]$ and $T > 0$.

When $T \geq K$, we prove a general result for maps f satisfying assumption **(A)**. To this end, we shall use the following auxiliary result:

Lemma 3 (El-Morshedy and Jiménez López 2008, Theorem B) *Assume that $f : (0, \infty) \to (0, \infty)$ has a globally attracting equilibrium p. Let $g : (0, \infty) \to (0, \infty)$ be a continuous map satisfying that $x < g(x) \leq \max\{f(x), p\}$ for all $x < p$, and $x > g(x) \geq \min\{f(x), p\}$ for all $x > p$. Then p is a globally attracting equilibrium of g.*

Proposition A.3 *Assume that f satisifies* **(A)**. *If $T \geq K$ and K is a global attractor of* (2.1)*, then K is a global attractor of* (2.3) *for all $q \in (0, 1]$.*

Proof If $T \geq K$, then Lemma 3 applies to $g = F_q$ because $x < F_q(x) \leq f(x) \leq \max\{f(x), K\}$ for all $x < K$, and $x > F_q(x) = f(x) \geq \min\{f(x), K\}$ for all $x > K$ (see Fig. 2a). □

Next we address the case $T < 1$ for the Ricker map.

Proposition A.4 *If $r \leq 2$ and $T < 1$, then the unique positive equilibrium $K_1 = K_1(q, T)$ of* (2.3) *with the Ricker map $f(x) = x\,\mathrm{e}^{r(1-x)}$ is globally asymptotically stable.*

Proof It is well known that the equilibrium $K = 1$ for the Ricker map $f(x) = x\,\mathrm{e}^{r(1-x)}$ is a global attractor if and only if $r \leq 2$ (e.g. Thieme 2003). Moreover, since $f''(x) < 0$ for all $x < 2/r$, it follows that $f''(x) < 0$ for all $x \in (0, 1)$ if $r \leq 2$. Thus, Propositions A.1 and A.2 ensure that (2.3) has a unique positive equilibrium K_1, and it is locally asymptotically stable if $T < 1$ and $q \in (0, 1)$.

Next we prove that K_1 is actually a global attractor. To this end, we use an enveloping theorem due to Cull (2007, Theorem 3). We have to show that $F(x) < 2K_1 - x$ if $x < K_1$, and $F(x) > 2K_1 - x$ if $x > K_1$.

Denote by p_1, p_2 the points such that $f(p_1) = f(p_2) = T$, $0 < p_1 < T < K_1 < 1 < p_2$. F is differentiable in (p_1, p_2). We distinguish three cases (see Fig. 11):

- If $x \in (0, p_1)$, then $F(x) = f(x) \leq T < 2T - x < 2K_1 - x$.
- If $x \in (p_2, \infty)$, then we use that $f(x) > 2 - x$ for all $x > 1$ (e.g. Cull 2007) to show that $F(x) = f(x) > 2 - x > 2K_1 - x$.
- If $x \in (p_1, p_2)$ we have $F'(x) = (1 - q) f'(x) > -1$, which makes it impossible that there is a point $q \in (p_1, K_1) \cup (K_1, p_2)$ such that $F(q) = 2K_1 - q$ (assume that such q exists, and apply Rolle's Theorem to the map $G(x) = 2K_1 - x - F(x)$ and the points q and K_1 to arrive at a contradiction).

Thus, F must remain below the line $2K_1 - x$ for $x < K_1$, and above it for $x > K_1$, and the proof is complete. □

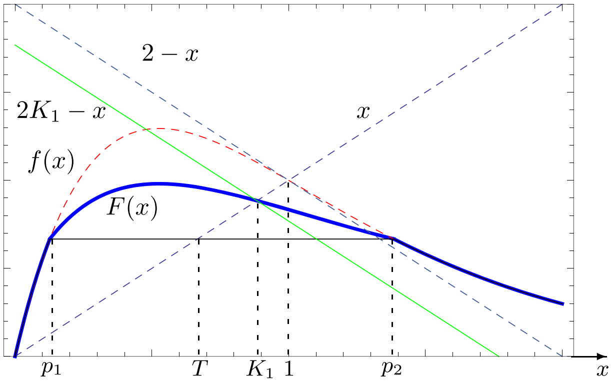

Fig. 11 A diagram showing how the modified map $F(x) = \min\{f(x), (1-q)f(x)+qT\}$ (solid blue line) is enveloped by the line $2K_1 - x$. The original Ricker map $f(x)$ is shown in a red dashed line (color figure online)

A.5 Stability switches for (2.3) with an unstable Ricker map

Here we rigorously prove the results about the Ricker model stated in Sect. 3.2.

Proposition A.5 *Assume that* $r > 2$, $0 \le T < 1$, *and* $q \in (0, 1)$.

(I) *The positive equilibrium* K_1 *of* (2.3) *with* $f(x) = x\,\mathrm{e}^{r(1-x)}$ *is asymptotically stable if and only if the following inequality holds:*

$$(1-q)(rg(r,q,T)-1) \le \mathrm{e}^{r(g(r,q,T)-1)}, \tag{A.2}$$

where

$$g(r,q,T) := \frac{2 + rqT + \sqrt{(rqT)^2 + 4}}{2r} \tag{A.3}$$

is the larger root of the quadratic equation $rx^2 - (2 + rqT)x + qT = 0$.

(II) *Moreover, for each* $r > 2$ *fixed, the boundary of the stability region defined by the implicit equation*

$$(1-q)(rg(r,q,T)-1) = \mathrm{e}^{r(g(r,q,T)-1)}$$

defines a decreasing curve $q = q(T)$ *in the plane* (T, q), $0 < T < 1$.

Proof We first prove **(I)**. Since the positive equilibrium K_1 of (2.3) belongs to the interval $(T, 1)$, function F is defined as $F(x) = (1-q)f(x) + qT$ in a neighborhood of K_1. This map is unimodal, of class C^3, and has a negative Schwarzian derivative everywhere. Thus, the condition for local asymptotic stability is $F'(K_1) \ge -1$, which is equivalent to $(1-q)f'(K_1) \ge -1$ (see Liz 2010). In order to get the stability boundary, we solve the system of equations

$$x = (1-q)f(x) + qT \tag{A.4}$$

$$-1 = (1-q)f'(x) \tag{A.5}$$

Since $f(x) = \mathrm{e}^{r(1-x)}$, system (A.4)–(A.5) reads

$$(1-q)\mathrm{e}^{r(1-x)} = \frac{x - qT}{x} \tag{A.6}$$

$$(1-q)\mathrm{e}^{r(1-x)} = \frac{-1}{1-rx} \tag{A.7}$$

This system leads to

$$\frac{x-qT}{x} = \frac{-1}{1-rx} \Longleftrightarrow rx^2 - (2 + rqT)x + qT = 0.$$

This quadratic equation has two positive roots

$$x_{\pm} = \frac{2 + rqT \pm \sqrt{(rqT)^2 + 4}}{2r}.$$

Since $0 < q < 1$, we get

$$2 - \sqrt{(rqT)^2 + 4} < 0 < 2rT(1-q),$$

which implies that $x_- < T$.

On the other hand, one can check that $x_+ = g(r, q, T) \in (T, 1)$ for some q such that

$$q < \frac{r-2}{(r-1)T} \quad \text{and} \quad q > \frac{rT-2}{rT-1} \quad \text{if } rT > 2.$$

Replacing $x = g(r, q, T)$ in (A.7), we get the boundary of the stability region defined in (A.2).

Next we prove **(II)**. The stability boundary can be written as $H(r, q, T) = 0$, where

$$H(r, q, T) = \mathrm{e}^{r(g(r,q,T)-1)} - (1-q)(rg(r, q, T) - 1).$$

We show that, for a fixed value of $r > 2$, it holds that $\partial H/\partial T$ and $\partial H/\partial q$ are positive at the equilibrium. Thus, the Implicit Function Theorem ensures that $\partial q/\partial T$ is negative, which proves **(II)**.

It is clear that $\partial g/\partial T > 0$ and $\partial g/\partial q > 0$, where g is defined in (A.3). On the other hand, it is evident that $rg(r, q, T) > 1$. Since

$$\frac{\partial H}{\partial T} = r\frac{\partial g}{\partial T}\left(\mathrm{e}^{r(g(r,q,T)-1)} - (1-q)\right),$$

$$\frac{\partial H}{\partial q} = r\frac{\partial g}{\partial q}\left(\mathrm{e}^{r(g(r,q,T)-1)} - (1-q)\right) + (rg(r, q, T) - 1)$$

it only remains to prove that $e^{r(g(r,q,T)-1)} > 1-q$.

Replacing $x = g(r, q, T)$ in (A.6), we get

$$(1-q)g(r,q,T)e^{r(1-g(r,q,T))} = g(r,q,T) - qT < g(r,q,T),$$

from where it follows that $(1-q)e^{r(1-g(r,q,T))} < 1$, as we wanted to prove. □

Corollary A.6 *Assume that $r > 2$, $0 \le T < 1$, and $q \in (0, 1)$. Denote by K_1 the positive equilibrium of (2.3) with $f(x) = x\,e^{r(1-x)}$.*

- **(i)** *For $T = 0$, K_1 is asymptotically stable if and only if $q \ge 1 - e^{2-r}$.*
- **(ii)** *As $T \to 1^-$, the limit form of the asymptotic stability condition for K_1 is given by the inequality $q > (r-2)/(r-1)$.*
- **(iii)** *For a given value of $T \in (0, 1)$, increasing q is stabilizing.*
- **(iv)** *For a fixed value of $q \in (0, 1)$, we have three cases:*
  - (a) *If $q \ge 1 - e^{2-r}$ ($r \le 2 - \ln(1-q)$), then K_1 is asymptotically stable, independently of T.*
  - (b) *If $(r-2)/(r-1) < q < 1 - e^{2-r}$, then increasing T is stabilizing.*
  - (c) *If $q \le (r-2)/(r-1)$ ($r \ge (2-q)/(1-q)$), then K_1 is unstable, independently of T.*

Proof **(i)** For $T = 0$, we have $g(r, q, T) = g(r, q, 0) = 2/r$, and therefore (A.2) reads $1 - q \le e^{2-r}$.

(ii) For $T = 1$, the solution of (A.4) is $x = 1$, and therefore the limit form of the asymptotic stability condition for K_1 as $T \to 1^-$ is given by $-1 < (1-q)f'(1) = (1-q)(1-r)$, which is equivalent to $q > (r-2)/(r-1)$.

(iii) and **(iv)** are a straightforward consequence of Proposition A.5 and the previous items **(i)** and **(ii)**.

□

A.6 Stability switches for (2.3) with a quadratic map

In this subsection we prove some analytic results for (2.3) with the quadratic map $f(x) = rx - (r-1)x^2$. By Proposition A.2, $r > 3$ is a necessary condition for the existence of a stability switch at the positive equilibrium K_1.

Proposition A.7 *Assume that $r > 3$, and $q \in (0, 1)$. As $T \to 1^-$, the limit form of the asymptotic stability condition for the equilibrium K_1 is given by the inequality $q > (r-3)/(r-2)$.*

Proof It is clear that the unique equilibrium of $F(x) = (1-q)f(x) + q$ is $K_1 = 1$. Thus, the limit form of the asymptotic stability condition is $-1 < (1-q)f'(1) = (1-q)(2-r)$, which is equivalent to $q > (r-3)/(r-2)$. □

A consequence of Propositions A.2 and A.7 is that, for a given value of $r > 3$, a necessary condition for the existence of a stability switch is $q < (r-3)/(r-2)$.

Proposition A.8 *Assume that $r > 3$, $0 \le T < 1$, and $q < (r-3)/(r-2)$.*

(I) *The boundary of the stability region of the positive equilibrium* K_1 *of* (2.3) *with* $f(x) = rx - (r-1)x^2$ *is implicitly defined by the equation*

$$((1-q)r-1)^2 + 4q(1-q)(r-1)T = 4. \tag{A.8}$$

Moreover, for each $r > 3$, (A.8) *defines an increasing curve* $q = q(T)$ *in the plane* (T, q), $0 < T < 1$.

(II) *In the limit case* $T = 0$*, the stability switch is defined by* $q = (r-3)/r$.

(III) *A stability switch as* T *is decreased occurs for all* q *such that*

$$\frac{r-3}{r} < q < \frac{r-3}{r-2}.$$

Proof **(I)** The positive equilibrium K_1 is the unique positive root of the quadratic equation $x = (1-q)f(x) + qT$, whose expression is

$$K_1 = \frac{(1-q)r - 1 + \sqrt{((1-q)r-1)^2 + 4q(1-q)(r-1)T}}{2(1-q)(r-1)}.$$

Notice that $q < (r-3)/(r-2)$ implies that $q < (r-1)/r$, and therefore $(1-q)r - 1 > 0$. A stability switch occurs when $(1-q)f'(K_1) = -1$, which leads to (A.8).

To show that $q = q(T)$ is increasing, we use implicit differentiation with the map

$$H(q, T) = ((1-q)r-1)^2 + 4q(1-q)(r-1)T - 4.$$

It is clear that $\partial H/\partial T > 0$ for all $r > 1$. On the other hand,

$$\partial H/\partial q = -2r((1-q)r-1) + 4T(r-1)(1-2q) < 0$$

if $q \geq 1/2$. If $q < 1/2$, since $T < 1$, we have

$$\begin{aligned}\partial H/\partial q &< -2r((1-q)r-1) + 4(r-1)(1-2q)\\ &= -2((1-q)r^2 - (3-4q)r + 2(1-2q)),\end{aligned}$$

and we can easily check that the last expression is negative for all $r > 3$.

Hence, $\partial q/\partial T = -(\partial H/\partial T)/(\partial H/\partial q) > 0$.

(II) For $T = 0$, (A.8) gives $(1-q)r - 1 = 2$, which is equivalent to $q = (r-3)/r$.

(III) is a consequence of **(II)** and Proposition A.7. □

A.7 Condition for the MSY in (2.3) with a Ricker map

Proposition A.9 *System* (4.1) *with* $f(x) = x\,\mathrm{e}^{r(1-x)}$ *has a solution* (x, T) *with* $x > 0$, $T \in (0, K)$*, if and only if* $r < q - \ln(1-q)$.

Proof For $T = 0$ and a fixed $q \in (0, 1)$, we can find the unique solution (r^*, x^*) of system (4.1). Indeed, system (4.1) with $T = 0$ becomes

$$f'(x) = 1; \qquad (1 - q) f(x) = x. \tag{A.9}$$

Using the expression of f in (A.9), we get

$$(1 - rx)\mathrm{e}^{r(1-x)} = 1 = (1 - q)\mathrm{e}^{r(1-x)},$$

which leads to $rx = q$. Replacing $x = q/r$ into $(1-q)\mathrm{e}^{r(1-x)} = 1$ gives $(1-q)\mathrm{e}^{r-q} = 1$, which is equivalent to $r = q - \ln(1 - q)$. Thus, the solution is $r^* = q - \ln(1 - q)$, $x^* = q/r^* = q/(q - \ln(1 - q))$.

Now, if $T > 0$, then system (4.1) leads to

$$(1 - rx)\mathrm{e}^{r(1-x)} = 1; \qquad (1 - q)x\mathrm{e}^{r(1-x)} + qT = x,$$

which, by elementary calculus, gives

$$rx = q\frac{x - T}{x - qT} := q_1 < q,$$

and therefore $r = q_1 - \ln(1 - q_1) < r^*$, since the map $v(q) = q - \ln(1 - q)$ is increasing for $q \in (0, 1)$. □

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