Effect of Delayed Harvesting on the Stability of Single-Species Populations

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Abstract New results on the impact of harvesting times and intensities on the stability properties of Seno population models are presented. Special attention is given to the global stability of the positive equilibrium in terms of the harvest timing.

1 Introduction

The moment of intervention is a key question in harvest programmes and is currently generating increasing interest. However, little is known about its effect on the population stability.

We used a discrete-time equation introduced by Hiromi Seno in [4] to model the dynamics of populations harvested at any time during the reproductive season. For a wide family of population models described by unimodal maps, we showed that for high harvesting efforts—below the threshold above which all populations go eventually extinct—the moment of the intervention does not affect the stability of the positive equilibrium, which acts as a global attractor.

For many population models involving the Ricker map, which has been shown to be a good descriptor of the dynamics of many populations, local stability implies global stability. We showed that this is also the case for the Ricker–Seno model.

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A. Korobeinikov et al. (eds.), *Extended Abstracts Spring 2018*,
Trends in Mathematics 11, https://doi.org/10.1007/978-3-030-25261-8_27

Additionally, we used this model to prove that timing can be stabilizing by itself. In other words, we showed that in some cases choosing an appropriate moment for removing individuals can induce an asymptotically stable positive fixed point in populations for which the same equilibrium would be unstable in case of triggering the intervention at the beginning or at the end on the reproductive season.

Our last result consists of pointing out that timing can be destabilizing for certain maps. We obtained specific mathematical counterexamples proving that Conjecture 3.5 in [1] is false.

2 Harvesting Model with Timing

Consider the discrete-time single-species population model

$$x_{t+1} = g(x_t)x_t, \tag{1}$$

where $x_t \in [0, \infty)$ is the population size at the beginning of the reproductive season t and $g\colon [0, \infty) \to \mathbb{R}$ is the per-capita production function. We are interested in populations satisfying the following conditions on g:

(i) $g'(x) < 0$ for all $x > 0$;
(ii) $g(0) > 1$;
(iii) there exists some $d > 0$ such that $xg(x)$ is strictly increasing on $(0, d)$ and strictly decreasing on (d, ∞).

Under these conditions, the dynamics are over-compensatory. On the other hand, harvesting a constant fraction $\gamma \in (0, 1)$ of the population at the end of every reproductive season corresponds to multiplication of the right-hand side of (1) by the survival fraction $(1 - \gamma)$,

$$x_{t+1} = (1 - \gamma)g(x_t)x_t. \tag{2}$$

Similarly, harvesting the same fraction at the beginning of the season leads to

$$x_{t+1} = g((1 - \gamma)x_t)(1 - \gamma)x_t. \tag{3}$$

In [4], Seno puts forward the following harvesting model, which encompasses the *limit* situations (2) and (3) by allowing the population to be harvested at any fixed point in time within the season. It reads

$$x_{t+1} = [\theta g(x_t) + (1 - \theta)g((1 - \gamma)x_t)](1 - \gamma)x_t, \tag{4}$$

where $\theta \in [0, 1]$ corresponds to the fixed harvesting moment. See [4] for a more detailed explanation and a graphical scheme of the population dynamics of this model.

Following the notation of [1], we rewrite the right-hand side of (4) as

$$\theta F_1(x_t) + (1-\theta)F_0(x_t) := F_\theta(x_t),$$

where $F_1(x) := (1-\gamma)g(x)x$ and $F_0(x) := g((1-\gamma)x)(1-\gamma)x$. Model (4) includes models (2) and (3) as special cases. Taking $\theta = 1$ corresponds to harvesting when the season ends, and $\theta = 0$ when it begins.

Over-compensatory models can exhibit positive unstable equilibria, which leads to fluctuating dynamics. We start by recalling a sufficient and necessary condition for the existence of such an equilibrium regardless of the intervention moment θ.

Proposition 1 (from Proposition 3.1 in [1]) *Assume that conditions (i)–(iii) hold. System (4) has a unique positive equilibrium (denoted by $K_\gamma(\theta)$) if and only if*

$$\gamma < \gamma^* := 1 - \frac{1}{g(0)}.$$

3 Results

3.1 Timing Does Not Affect Stability for High Harvesting Efforts

We showed that the asymptotic stability of $K_\gamma(0)$ implies the asymptotic stability of $K_\gamma(\theta)$ for $\theta \in [0, 1]$ if γ is chosen close enough to γ^* and g satisfies conditions (i)–(iii). Moreover, we obtained that $K_\gamma(\theta)$ is not only asymptotically stable, but attracts all solutions of (4) starting with a positive initial condition.

Proposition 2 *Assume that conditions (i)–(iii) hold. Then, there exists $\gamma_0 < \gamma^*$ such that for $\gamma \in [\gamma_0, \gamma^*)$ the fixed point $K_\gamma(\theta)$ of (4) is asymptotically stable for all $\theta \in [0, 1]$ and all positive solutions of (4) converge to $K_\gamma(\theta)$.*

3.2 Global Stability for Any Harvesting Time in the Ricker Case

Proposition 2 gives a sufficient condition for the global stability of the positive equilibrium of (4) in the Ricker case, for which $g(x) = \exp(r(1-x))$. But as the growth parameter r increases, the harvesting intensity has to be chosen higher and very close to the threshold $\gamma^* = 1 - e^{-r}$ above which all populations go extinct. This has two important drawbacks: (1) selecting harvesting efforts near such a threshold could be considered dangerous, and (2) attaining high harvesting intensities may be difficult in case of constraints of harvesting/thinning management. The following result proves that for the Ricker model the asymptotic stability of $K_\gamma(0)$ implies global stability of $K_\gamma(\theta)$ for all $\theta \in [0, 1]$.

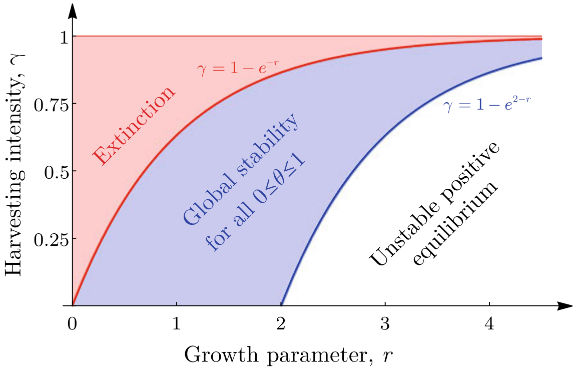

Fig. 1 In the blue area changing timing does not affect the global attraction of the positive equilibrium of model (4) for the Ricker map

Theorem 3 *Assume* $g(x) = e^{r(1-x)}$, $r > 0$, *and* $\gamma \in (0, 1)$ *such that* $1 - e^{2-r} \leq \gamma < 1 - e^{-r}$. *Then, for any* $\theta \in [0, 1]$, *the positive equilibrium of Eq.* (4) *is G.A.S.*

Figure 1 illustrates the region of parameters (r, γ) for which changing timing does not affect the global attraction of the positive equilibrium according to Theorem 3.

3.3 Timing Can Be Stabilizing by Itself

We proved that in the Ricker case it is possible to find $\theta \in (0, 1)$ such that $K_\gamma(\theta)$ for (4) is stable when $K_\gamma(0)$ is unstable.

Proposition 4 *Assume* $g(x) = e^{r(1-x)}$ *and* $r > 0$. *Then, there exists* $\gamma_c < \gamma_* := 1 - e^{2-r}$ *such that for any* $\gamma \in (\gamma_c, \gamma_*)$ *it is possible to find a timing interval* (θ_0, θ_1) *with the property that for each* $\theta \in (\theta_0, \theta_1)$ *the fixed point* $K_\gamma(\theta)$ *is asymptotically stable for* (4).

3.4 Timing Can Be Destabilizing

Proposition 4 shows that timing can be stabilizing by itself. In view of this, it is logical to ask the opposite question: *can timing be destabilizing?* Cid et al. conjectured in [1] that harvesting times θ in the interior of [0, 1] cannot be destabilizing if conditions (i)–(iii) are satisfied.

Conjecture 5 ([1, Conj. 3.5]) *Assume that conditions (i)–(iii) hold. If the positive equilibrium* $K_\gamma(0)$ *of* (4) *with* $\theta = 0$ *is asymptotically stable, then the fixed point* $K_\gamma(\theta)$ *is asymptotically stable for* (4) *for all* $\theta \in [0, 1]$.

A counterexample of this conjecture corresponds to the analytic function

$$g(x) = e^{6-15x+15x^2-\frac{11}{2}x^3}, \tag{5}$$

for which $\frac{dF_{0.6}}{dx}(K_{0.5}(0.6)) = F'_{0.6}(K_{0.5}(0.6)) \approx -1.278$ while $F'_0(K_{0.5}(0)) = F'_1(K_{0.5}(1)) \approx -0.207$.

4 Discussion and Conclusions

We studied the combined effect of harvesting intensity and harvesting time on the stability of a discrete population model proposed by Seno [4]. Under general conditions, we showed that timing has no negative effect on the stability of the positive equilibrium if the harvesting intensity is close enough to γ^*. Moreover, we proved that the latter stability is global. To the best of our knowledge, this is the first global stability result for (4) valid for general over-compensatory population models, since global stability results in [1] only cover under-compensatory models (such as the Beverton–Holt model) and the quadratic model.

For the Ricker–Seno model, we proved that there is global stability of the positive equilibrium regardless of the time of the intervention. Additionally, we showed that for this model timing can be stabilizing, that is, a harvesting intensity applied at an appropriate time of the season can asymptotically stabilize the positive equilibrium even when it cannot be stabilized at the beginning or at the end of the reproductive season with the same harvesting intensity.

Finally, we showed that timing can be destabilizing under natural conditions assumed on population production maps. This provides counterexamples for a conjecture recently published in [1]. However, these counterexamples are the result of mathematical constructions. Most of the population maps considered in the ecological literature satisfy additional conditions, as for example to have negative Schwarzian derivative, which may prevent any destabilizing effects of timing.

Our study leaves several open questions for future research. First, to find what extra conditions are necessary for Conjecture 5 to hold. Second, to provide general conditions for which timing is stabilizing by itself for population models different from the Ricker model.

Further details and proofs of the results provided here can be found in [2, 3].

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