The discrete Beverton-Holt model with periodic harvesting in a periodically fluctuating environment*

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Abstract

In this paper, we investigate the effect of constant and periodic harvesting on the Beverton-Holt model in a periodically fluctuating environment. We show that in a periodically fluctuating environment, periodic harvesting gives a better maximum sustainable yield compared to constant harvesting. However, if one can also fix the environment, then constant harvesting in a constant environment can be a better option, especially for sufficiently large initial populations. Also, we investigate the combinatorial structure of the periodic sequence of carrying capacities and its effect on the maximum sustainable yield. Finally, we leave some questions worth further investigations.

Keywords: Periodic Beverton-Holt model; periodic harvesting; periodic solutions.
Mathematics Subject Classification (2000): 39A11; 92D25; 92B99.

1 Introduction

In October 2008, the World Bank and the Food and Agriculture Organization of the United Nations released a study on the economic justification for fisheries reform [17]. The title of the report says it all "The Sunken Billions." The report argues that the sunken \$50 Billions is a conservative estimate for the losses incurred annually due to the business as usual way of fishing. In general, the study shows a grim picture on the current state of marine fish stocks. The recovery of the sunken billions and wasted harvesting efforts is obviously not an instantaneous process, but rather the product of two main strategies: reducing harvesting efforts and rebuilding of fish stocks. Clearly, the two are very well related; however, a good understanding of theoretical harvesting strategies on population models will go along way in designing an optimal strategy.

There is a wealth of research on the effect of harvesting on the dynamics of populations governed by differential equations. For example, in predator prey systems, constant harvesting can lead to the destabilization of population's equilibria, the creation of limit cycles,

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different types of bifurcations, catastrophe and even chaotic behavior [5, 9, 10, 15, 20, 25]. Optimal harvesting for single species have been studied by several authors from different points of view, see for example [23, 26, 28] and the references therein. Recently, Braverman and Mamadani [7] considered both autonomous and non-autonomous population models and found that constant harvesting is always superior to impulsive harvesting even though impulsive harvesting can sometimes do as good as constant harvesting. Their results contrast with the results of Ludwig [19] and Xu et. al [27]. For single species, Ludwig [19] studied models with random fluctuations and found that constant effort harvesting does worse than other harvesting strategies. Xu et. al [27] investigated harvesting in seasonal environments of a population with logistic growth and found that pulse harvesting is usually the dominant strategy and that the yield depends dramatically on the intrinsic growth rate of population and the magnitude of seasonality. Furthermore, for large intrinsic growth rate and small environmental variability several strategies such as constant exploitation rate, pulse harvest, linear exploitation rate, and time-dependent harvest are quite effective and have comparable maximum sustainable yields. However, for populations with small intrinsic growth rate but subject to large seasonality none of these strategies is particularly effective, but still pulse harvesting provides the best maximum sustainable yield.

Although the subject of difference equations and discrete models has been flourishing in the past two decades, harvesting in discrete population models is relatively morbid. Constant rate depletion on the discrete Ricker model was studied in [21], where it was shown numerically that populations exhibiting chaotic oscillations are not necessarily vulnerable to extinction. The effect of periodic harvesting on the discrete Ricker model and for a host-parasite model was studied in [11]. The stochastic Beverton-Holt equation with constant and proportional harvesting was studied in [6]. A special type of periodic impulsive harvesting in relation with seasonal environment was also studied in [22]. In [4], AlSharawi and Rhouma examined the effect of harvesting and stocking on competing species governed by a Leslie/Gower model and found that careful harvesting of the dominant species in an exclusive competitive environment can sometimes lead to the survival of the weaker species. More recently, the authors have also studied the Beverton-Holt equation under periodic and conditional harvesting and have found that in a constant capacity environment, constant rate harvesting is the optimal strategy [3].

This paper is a continuation of [3], and it is a modest contribution toward a full understanding of harvesting strategies on discrete population models. We compare the effect of different harvesting strategies in different environments. In particular, we consider and compare the effect of periodic and constant harvesting in both constant and periodic environments in a population governed by the Beverton-Holt model

$$y_{n+1} = \frac{\mu k_n y_n}{k_n + (\mu - 1)y_n}, \quad n \in \mathbb{N} := \{0, 1, 2, \ldots\}, x_0 \in \mathbb{R}^+, \tag{1.1}$$

where $\mu > 1$ is the population inherent growth rate and k_n is the population carrying capacity at time n. In our analysis, we focus on the maximum sustainable yield commonly known as the MSY [12]. Despite its disregard to cost, the MSY remains the main criteria for managing populations and avoiding over exploitation.

The paper is structured as follows: In sections 2 and 3, we discuss the existence of periodic solutions, the basin of attraction of a stable periodic solution, and we address different aspects of constant yield harvesting in periodic environment. In section 4, we focus on periodic harvesting in periodic environments and its effect on population's resonance/attentuance. We make a comparison with other harvesting strategies, and give a concrete discussion when $p = 2$. Finally, we close the paper with a brief conclusion and a few questions that worth further investigation.

2 Constant yield harvesting in a periodic environment

In this section, we investigate the effect of constant harvesting on Eq. (1.1) with periodically fluctuating carrying capacities. Thus, we have

$$x_{n+1} = f_n(x_n) := \frac{\mu k_n x_n}{k_n + (\mu - 1)x_n} - h\,, \qquad k_{n+p} = k_n,\ n \in \mathbb{N} \tag{2.1}$$

where h is the constant intensity of harvesting. Since when $h = 0$, $\mu > 1$ is a necessary condition for a population to persist, we always assume $\mu > 1$. Also, observe that $f_j(x)$ is asymptotic to $\frac{\mu k_j}{\mu-1}$. So, it is obvious that $0 \le h \le h_{\max} < \min\{\frac{\mu}{\mu-1}k_j, j = 0, 1, \ldots, p-1\}$, where $h_{\max}$ is a threshold level of harvesting that needs to be investigated. The next result gives an upper bound on the maximal harvesting level $h_{\max}$.

Proposition 2.1. *Consider Eq. (2.1), then*

$$h_{\max} < \min\left\{ \left(\sum_{j=0}^{p-1} \mu^j\right) \left(\sum_{j=0}^{p-1} \frac{\mu^j}{k_{j+i \bmod p}}\right)^{-1}, i = 0, 1 \ldots, p-1 \right\}.$$

PROOF: The set on the right hand side of the inequality is the stable cycle at zero harvesting level. □

Define the maps $F_0(x) = Id(x) = x$ and $F_n(x) = f_{(n-1) \bmod p}(F_{n-1}(x))$ for all $n \in \mathbb{Z}^+$. The orbits of Eq. (2.1) take the form

$$\mathcal{O}(x_0) = \{x_0, F_1(x_0), F_2(x_0), \ldots, F_{p-1}(x_0), \ldots\}. \tag{2.2}$$

For each $j = 0, \ldots, p-1$, define the matrix

$$B_j := \begin{bmatrix} k_j & \mu - 1 \\ -hk_j & \mu k_j - h(\mu - 1) \end{bmatrix} \tag{2.3}$$

and consider the operators $T_j(X_0) = B_j X_0$, where $X_0 = [1, x_0]^T$. A simple induction argument shows that orbit (2.2) takes the matrix form

$$\mathcal{O}^+(X_0) = \{X_0, \mathcal{B}_1 X_0, \mathcal{B}_2 X_0, \ldots, \mathcal{B}_{p-1} X_0, \ldots\}, \tag{2.4}$$

where $\mathcal{B}_0 = I$ and $\mathcal{B}_n = B_{n-1}\mathcal{B}_{n-1}$. For more details about this approach, we refer the reader to [3].

Proposition 2.2. *Each of the following holds true for Eq. (2.1):*

(i) If $\operatorname{tr}(\mathcal{B}_p) > 2\mu^{\frac{p}{2}} \prod_{j=0}^{p-1} k_j$*, then there exist two* p*-cycles; One of them is stable and the other is unstable.*

(ii) If $\operatorname{tr}(\mathcal{B}_p) = 2\mu^{\frac{p}{2}} \prod_{j=0}^{p-1} k_j$*, then exactly one semi-stable* p*-cycle exists.*

(iii) If $\operatorname{tr}(\mathcal{B}_p) < 2\mu^{\frac{p}{2}} \prod_{j=0}^{p-1} k_j$*, then there are no periodic solutions, and consequently, no population persists.*

PROOF: It follows along the same lines as the proof of Theorem 3.3 in [3]. □

By now, it is well known that periodic environment does not enhance populations governed by the Beverton-Holt model with constant growth rate and periodic capacity [13, 14, 16, 18]. This suggests that periodic environment has a negative impact on the maximum harvesting level. Indeed, we have the following result:

Theorem 2.1. *The maximum harvesting level* $h_{\max}$ *in a periodic environment is less than the maximum harvesting level in a constant environment with* $k = k_{av} := \frac{1}{p}\sum_{j=0}^{p-1} k_j$*.*

PROOF: Let $\{\bar{x}_0, \bar{x}_1, \ldots, \bar{x}_{p-1}\}$ be the semi-stable p-cycle assured at the maximum harvesting level $h_{\max}$. From Eq. (2.1), we obtain

$$\sum_{j=0}^{p-1} x_j = -ph_{\max} + \sum_{j=0}^{p-1} \frac{k_j \mu x_j}{k_j + (\mu - 1)x_j}$$

and thus

$$h_{\max} = \frac{1}{p}\sum_{j=0}^{p-1}\left(\frac{k_j \mu x_j}{k_j + (\mu - 1)x_j} - x_j\right).$$

Since the map $h_j(t) = \frac{k_j \mu t}{k_j + (\mu-1)t} - t,\ t > 0$ has absolute maximum at $t = \frac{(\sqrt{\mu}-1)}{\mu-1}k_j$, then

$$h_{\max} < \frac{1}{p}\frac{(\sqrt{\mu}-1)^2}{(\mu-1)}\sum_{j=0}^{p-1} k_j = \frac{(\sqrt{\mu}-1)^2}{(\mu-1)}k_{av}. \tag{2.5}$$

The right hand side of the inequality is the maximum harvesting level at the constant carrying capacity $k = k_{av}$, which completes the proof. □

3 Harvesting levels and the basin of attraction

It is well known [13, 16] that for $h = 0$, system (2.1) has a globally asymptotically stable p-cycle, i.e., the basin of attraction of the p-cycle is $\mathbb{R}^+$. In this section, we consider Eq. (2.1) with $0 < h \leq h_{\max}$ and investigate the basin of attraction of the stable/semi-stable p-cycle. But first, we give a few necessary definitions. A solution of Eq. (2.1) is called persistent if the corresponding initial population survives indefinitely. Here, it is worth emphasizing that although one can start iterating Eq. (2.1) at any time $n = n_0$, time reference is crucial in our analysis, and an initial population is meant x_0 all the time. A set $\mathcal{D}_h := \{x : \ x \in \mathbb{R}^+\}$ is persistent if each solution of Eq. (2.1) with $x_0 \in \mathcal{D}_h$ is persistent. It is called the persistent set if it is the largest persisting set at the harvesting level h. Thus, a persistent set must contain the basin of attraction of the stable p-cycle assured by Proposition 2.2.

Proposition 3.1. *Let $0 < h \leq h_{\max}$ and $\{\bar{x}_{0,l}, \bar{x}_{1,l}, \ldots, \bar{x}_{p-1,l}\}$ be the unstable p-cycle. Then $\mathcal{D}_h = [\bar{x}_{0,l}, \infty)$.*

PROOF: Let $x_0 \geq \bar{x}_{0,l}$. From the monotonicity of the maps $f_j, j = 0 \ldots, p-1$, we obtain $x_{n+1} \geq \bar{x}_{n \bmod p, l} > 0$ for all $n \in \mathbb{N}$. Thus $[\bar{x}_{0,l}, \infty) \subseteq \mathcal{D}_h$. Now, if $x_0 < \bar{x}_{0,l}$, then $x_{n+1} = F_{p-1}(x_0)$ and the monotonicity of F_{p-1} implies $x_{p+1} < \bar{x}_{0,l}$. For sufficiently large n, $x_{np+1} = F^n_{p-1}(x_0) < 0$, which completes the proof. $\square$

Proposition 3.2. *Suppose that $h \leq \dfrac{(\sqrt{\mu}-1)^2 k_j}{(\mu - 1)}$ for all $j = 0, \ldots, p-1$, and let $s_{l,j} \leq s_{r,j}$ be the fixed points of the map f_j. Then,*

$$[\max\{s_{l,j}, j = 0, \ldots, p-1\}, \infty) \subseteq \mathcal{D}_h \quad \textit{and} \quad \mathcal{D}_h \subseteq [\min\{s_{l,j-1}, j = 0, \ldots, p-1\}, \infty).$$

PROOF: Since $h \leq (\sqrt{\mu}-1)^2 k_j/(\mu - 1)$ for each j, then each map f_j has two fixed points $s_{l,j} \leq s_{r,j}$. Now, trace the iterates of Eq. (2.1) for a given initial condition x_0 to obtain the result. $\square$

If we have complete control over the carrying capacities in the p-periodic sequence $\{k_j\}$, then Theorem 2.1 shows that we can achieve a maximum harvesting level by taking a constant carrying capacity, i.e., $p = 1$. However, assume we do not have this absolute power, but we have a flexible control over the periodic permutation of the carrying capacities $\{k_j\}$. In other words, we are considering a difference equation of the form

$$x_{n+1} = f_{j_n}(x_n) := \frac{k_{j_n}\mu x_n}{k_{j_n} + (\mu - 1)x_n} - h, \quad n \in \mathbb{N}, \tag{3.1}$$

where $\{j_0, j_1, \ldots, j_{p-1}\}$ is a permutation of $\{0, 1, 2, \ldots, p-1\}$ and $k_{j_{n+p}} = k_{j_n}$ for all positive integers n. Under these circumstances, we give the next result.

Theorem 3.1. *Fix a set of carrying capacities $\{k_0, k_1, \ldots, k_{p-1}\}$. All equations of the form (3.1) with permutations $(j_0, j_1, \ldots, j_{p-1})$ in the dihedral group of order p give same maximum constant harvesting level.*

PROOF: The maximum harvesting level is the smallest positive solution of the equation

$$\operatorname{tr}(B_{j_p} B_{j_{p-1}} \cdots B_{j_0}) - 2\mu^{\frac{p}{2}} k_0 k_1 \cdots k_{p-1} = 0.$$

Now, the elements of the dihedral group D_p are rotations and reflections. The rotations are assured by the trivial trace property $\operatorname{tr}(B_{j_i} B_{j_k}) = \operatorname{tr}(B_{j_k} B_{j_i})$. For the reflections, we need to show that

$$\operatorname{tr}(B_{j_{p-1}} B_{j_{p-2}} \ldots B_{j_0}) = \operatorname{tr}(B_{j_0} B_{j_1} \ldots B_{j_{p-1}}). \tag{3.2}$$

First, we rewrite the matrix B_{j_i} in Eq. (2.3) as $B_{j_i} = k_{j_i}A + (\mu - 1)C$, where

$$A := \begin{bmatrix} 1 & 0 \\ -h & \mu \end{bmatrix} \quad \text{and} \quad C := \begin{bmatrix} 0 & 1 \\ 0 & -h \end{bmatrix}.$$

By simple induction, we can show that

$$A^n = \begin{bmatrix} 1 & 0 \\ & \\ -h\frac{(\mu^{n+1}-1)}{\mu-1} & \mu^n \end{bmatrix} \quad \text{and} \quad C^n = (-h)^{n-1}C.$$

Now, let $\mathcal{P}$ be the power set of $\{0, 1, \ldots, p-1\}$. We expand the product of the matrices B_{j_i} and write

$$\begin{aligned}
\mathrm{tr}\,(B_{j_{p-1}}B_{j_{p-2}}\cdots, B_{j_0}) &= \sum_{S\in\mathcal{P}}(\mu-1)^{p-|S|}\prod_{i\in S}k_{j_i}\mathrm{tr}\,(D(S)),\\
\mathrm{tr}\,(B_{j_0}B_{j_1}\cdots, B_{j_{p-1}}) &= \sum_{S\in\mathcal{P}}(\mu-1)^{p-|S|}\prod_{i\in S}k_{j_i}\mathrm{tr}\,(\hat{D}(S)),
\end{aligned}$$

where $|S|$ is the cardinality of the set S and

$$\begin{aligned}
D(S) &= D_{p-1}(S)D_{p-2}(S)\cdots D_1(S)D_0(S),\\
\hat{D}(S) &= D_0(S)D_1(S)\cdots D_{p-2}(S)D_{p-1}(S)
\end{aligned}$$

and

$$D_j(S) = \begin{cases} A & \text{if } j \in S \\ C & \text{otherwise.} \end{cases}$$

Now, proving Eq. (3.2) is equivalent to proving that

$$\mathrm{tr}\,(D_{p-1}(S)D_{p-2}(S)\cdots D_0(S)) = \mathrm{tr}\,(D_0(S)D_1(S)\cdots D_{p-1}(S)).$$

This is obvious if S is either the empty or the complete set $\{0, 1, \ldots, p-1\}$. If S is a nonempty proper subset of $\{0, 1, \ldots, p-1\}$, then $D(S)$ contains the product of at least one matrix A and one matrix C. Thus, using the rotation property, we can write

$$\mathrm{tr}\,(D(S)) = \mathrm{tr}\,(A^{\alpha_1}C^{\beta_1}A^{\alpha_2}C^{\beta_2}\cdots A^{\alpha_m}C^{\beta_m}) = (-h)^{-m+\sum\beta_i}\mathrm{tr}\,(A^{\alpha_1}CA^{\alpha_2}C\cdots A^{\alpha_m}C)$$

for some positive integers $\alpha_1\cdots, \alpha_m, \beta_1, \cdots, \beta_m$ that satisfy $\sum\alpha_i = |S|$ and $\sum\beta_i = p-|S|$. Since

$$A^{\alpha_i}C = \begin{bmatrix} 0 & 1 \\ 0 & \gamma_{\alpha_i} \end{bmatrix}, \quad \gamma_{\alpha_i} = -\frac{(\mu^{\alpha_i+1}-1)h}{\mu-1},$$

then

$$\mathrm{tr}\,(D(S)) = (-h)^{-m+\sum\beta_i}\prod_{i=1}^{m}\gamma_{\alpha_i}.$$

On the other hand,

$$
\begin{aligned}
\operatorname{tr}(\hat{D}(S)) &= \operatorname{tr}(C^{\beta_m}A^{\alpha_m}...C^{\beta_2}A^{\alpha_2}C^{\beta_1}A^{\alpha_1}) \\
&= \operatorname{tr}(A^{\alpha_m}...C^{\beta_2}A^{\alpha_2}C^{\beta_1}A^{\alpha_1}C^{\beta_m}) \\
&= (-h)^{-m+\sum\beta_i}\operatorname{tr}(A^{\alpha_m}C...A^{\alpha_2}CA^{\alpha_1}C) \\
&= (-h)^{-m+\sum\beta_i}\prod_{i=1}^{m}\gamma_{\alpha_i},
\end{aligned}
$$

which completes the desired proof. □

Next, we give the polynomials $\operatorname{tr}(\mathcal{B}_p)$ for $p = 2, 3, 4$, whose lowest positive root give the maximal constant harvesting level in a periodic environment, then we give an illustrative example.

$$
\begin{aligned}
\operatorname{tr}(\mathcal{B}_2) &= (1-\mu)^2h^2 - (\mu-1)(\mu+1)(k_0+k_1)h + k_1k_0(\mu^2+1) \\
\operatorname{tr}(\mathcal{B}_3) &= -(\mu-1)^3(h)^3 + (\mu+1)(\mu-1)^2h^2\left(\sum_{j=0}^{2}k_j\right) \\
&\quad -h\left((\mu^3-1)\sum_{i=0}\sum_{j=i+1}^{2}k_ik_j\right) + k_2k_1k_0(\mu^3+1) \\
\operatorname{tr}(\mathcal{B}_4) &= (\mu-1)^4h^4 - (\mu+1)(\mu-1)^3h^3\left(\sum_{j=0}^{3}k_j\right) \\
&\quad +(\mu-1)^2h^2\left(\mu(k_0k_2+k_1k_3) + (\mu^2+\mu+1)\sum_{j=0}^{2}\sum_{i=j+1}^{3}k_jk_i\right) \\
&\quad -(\mu^4-1)k_0k_1k_2k_3h\left(\sum_{j=0}^{3}\frac{1}{k_j}\right) + (\mu^4+1)k_0k_1k_2k_3.
\end{aligned}
$$

Example 3.1. *(i) Consider the case $p = 2$, $k_0 = 1, k_1 = 4$ and $\mu = 4$. Then the value of $h_{\max} = \frac{1}{6}(25 - \sqrt{481})$ and the semi-stable 2-cycle is $\{\bar{y}_0 = \frac{1}{30}(\sqrt{481} - 1), \bar{y}_1 = \frac{2}{15}(\sqrt{481} - 19)\}$ with the interval $[\frac{1}{30}(\sqrt{481} - 1), \infty)$ as the basin of attraction. Changing the order of the carrying capacities to $k_0 = 4, k_1 = 1$, does not change the value of $h_{\max}$, but it does in return extend the basin of attraction to $[\frac{2}{15}(\sqrt{481} - 19), \infty)$. In fact, for constant harvesting in periodic environment with $p = 2$, the order of carrying capacities does not affect $h_{\max}$, but $k_0 \geq k_1$ will enlarge the basin of attraction.*

(ii) For $p = 3$, the order of $\{k_j\}$ does not change h_{max}. This is a little striking since, in the absence of harvesting the order of $\{k_j\}$ does change the average population. In fact, if $\mu = 4, k_0 = 1/2$, $k_1 = 2$ and $k_2 = 30$ and in the absence of harvesting, the average population is $\bar{y} = 2.195$ which is 31.34% more than the average population

of $\bar{y} = 1.671$ *obtained if the carrying capacities were presented in the order* $k_0 = 30$, $k_1 = 2$ *and* $k_2 = 1/2$. *The difference between the two populations is actually as high as* 83% *if* $\mu = 16$.

(iii) For $p = 4$, *there are 24 permutations of* $\{k_j\}$ *but the value of* $\mathrm{tr}\,(\mathcal{B}_4)$ *can only take three possible values. For each of these values there corresponds a value of* h_{max}. *For instance, if*

$$\{k_j\} = \{j + 10(1 + (-1)^j) : \ j = 0, 1, 2, 3\},$$

then $(k_0, k_1, k_2, k_3) = (20, 1, 22, 3), (3, 22, 1, 20)$ *and their cyclic permutation give* $h_{\max 3} = 0.932825$, $(k_0, k_1, k_2, k_3) = (20, 1, 3, 22), (22, 3, 1, 20)$ *and their cyclic permutation give* $h_{\max 2} = 0.892442$, *and* $(k_0, k_1, k_2, k_3) = (20, 3, 1, 22), (22, 1, 3, 20)$ *and their cyclic permutation give* $h_{\max 1} = 0.892846$. *Notice that the difference between the two extremes is about* 5%.

The next result shows which permutation would maximize the harvesting level for some values of p.

Theorem 3.2. *Consider Eq. (3.1) and assume the initial population is sufficiently large. Without loss of generality, let* $k_0 \leq k_1 \leq \cdots \leq k_{p-1}$. *Each of the following holds true:*

(i) For $p = 2$ *or* 3, *a permutation of the carrying capacities does not change the maximum harvesting level.*

(ii) For $p = 4$, *we can achieve three different levels of maximum harvesting through permutations of the carrying capacities. In particular,* $(j_0, j_1, j_2, j_3) = (0, 2, 1, 3)$ *or* $(3, 1, 2, 0)$ *and their cyclic permutations give the largest, and* $(j_0, j_1, j_2, j_3) = (3, 2, 0, 1)$ *or* $(1, 0, 2, 3)$ *and their cyclic permutation give the smallest.*

(iii) For $p = 5$, *we can achieve twelve different levels of maximum harvesting through permutations of the carrying capacities. In particular,* $(j_0, j_1, j_2, j_3) = (1, 2, 3, 0, 4)$ *or* $(4, 0, 3, 2, 1)$ *and their cyclic permutations give the largest, and* $(j_0, j_1, j_2, j_3) = (3, 1, 0, 2, 4)$ *or* $(4, 2, 0, 1, 3)$ *and their cyclic permutation give the smallest.*

PROOF: Since the maximum harvesting level for each permutation $(j_0, j_1, \ldots, j_{p-1})$ is achieved at

$$\mathrm{tr}\,(B_{j_{p-1}} B_{j_{p-2}} \cdots B_{j_1} B_{j_0}) = 2\sqrt{\det(B_{j_{p-1}} B_{j_{p-2}} \cdots B_{j_1} B_{j_0})} = 2\mu^{\frac{p}{2}} \prod_{i=0}^{p-1} k_i,$$

then we need to investigate the minimum positive value of h that satisfies this equation. (i) follows straight from the expressions of $\mathrm{tr}\,(\mathcal{B}_2)$ and $\mathrm{tr}\,(\mathcal{B}_3)$. To prove (ii), classify the 4! elements of the permutation group into three subgroups, each of which is isomorphic to the dihedral group of order 4. Now, Theorem 3.1 says that it is possible to obtain three different values of $h_{\max}$. More specifically, $(j_0, j_1, j_2, j_3) = (3, 2, 0, 1)$ or $(1, 0, 2, 3)$ and their cyclic permutations give the same maximum harvesting level, say $h_{\max 1}$. Similarly, $(j_0, j_1, j_2, j_3) = (0, 1, 2, 3)$ or $(3, 2, 1, 0)$ and their cyclic permutations give $h_{\max 2}$,

$(j_0, j_1, j_2, j_3) = (0,2,1,3)$ or $(3,1,2,0)$ and their cyclic permutations give $h_{\max 3}$. Now, we proceed to show that $h_{\max 1} \leq h_{\max 2} \leq h_{\max 3}$. Define

$$\begin{aligned} q_1(h) \;\; &: \;\; = \mathrm{tr}\,(B_3B_2B_0B_1) - 2\mu^2 k_3k_2k_1k_0, \\ q_2(h) \;\; &: \;\; = \mathrm{tr}\,(B_3B_2B_1B_0) - 2\mu^2 k_3k_2k_1k_0, \\ q_3(h) \;\; &: \;\; = \mathrm{tr}\,(B_3B_0B_2B_1) - 2\mu^2 k_3k_2k_1k_0, \end{aligned}$$

then $q_i(0) > 0$ and $q_i(h_{\max i}) = 0$ for $i = 1,2,3$. Furthermore, straightforward computations show that

$$\begin{aligned} q_3(h) &= q_2(h) + \mu(\mu-1)^2(k_1-k_2)(k_0-k_3)h^2, \\ q_3(h) &= q_1(h) + \mu(\mu-1)^2(k_1-k_3)(k_0-k_2)h^2, \\ q_1(h) &= q_2(h) + \mu(\mu-1)^2(k_3-k_2)(k_0-k_1)h^2. \end{aligned}$$

Now, $q_1(h_{\max 2}) \leq 0$ implies $h_{\max 1} \leq h_{\max 2}$, $q_1(h_{\max 3}) \leq 0$ implies $h_{\max 1} \leq h_{\max 3}$ and $q_2(h_{\max 3}) \leq 0$ implies $h_{\max 2} \leq h_{\max 3}$. The proof of (iii) is computational and too long; however, it follows along the same lines as the proof of (ii), and thus, we omit it. □

4 Periodic harvesting in a periodic environment

In this section, we force periodic harvesting on Eq. (2.1), and thus, we consider

$$x_{n+1} = f_n(x_n) := \frac{k_n\mu x_n}{k_n + (\mu-1)x_n} - h_n, \quad k_{n+p} = k_n, h_{n+p} = h_n, n \in \mathbb{N}. \tag{4.1}$$

We give some general results first, then we discuss resonance and attenuance. Finally, for the sake of concreteness, we focus on the specific case $p = 2$.

4.1 The general case

By considering the matrix of Eq. (2.3) to be

$$B_j := \begin{bmatrix} k_j & \mu - 1 \\ -hk_j & \mu k_j - h_j(\mu-1) \end{bmatrix}, \tag{4.2}$$

Proposition 2.2 continues to hold with the exception that cycles period may not be minimal, i.e., the cycle's period could be a divisor of p. This is due to the freedom in the two parameters k_j and h_j. For instance, consider $p = \mu = 4$ and

$$k_0 = \frac{1}{2}(9+3\sqrt{17}),\ k_1 = 9,\ k_3 = \frac{1}{4}(15+3\sqrt{57}), k_4 = \frac{1}{5}(3+2\sqrt{21}),\ h_j = \frac{3(k_j-1)}{k_j+3}.$$

In this case, $\bar{x} = 1$ is an equilibrium point and $\{\bar{x}_j = j+2\}_{j=0}^{3}$ is a 4-cycle. Furthermore, $[1, \infty)$ is the persistent set. For more details about the structure of periodic solutions in periodic discrete systems, we refer the reader to [1, 2].

In a constant capacity environment with $k = k_{av} = \dfrac{1}{p}\sum_{j=0}^{p-1} k_i$, the maximum constant harvesting is $h_{max} = \dfrac{(\sqrt{\mu}-1)^2}{\mu - 1}k_{av}$. The following theorem indicates that periodic harvesting in a periodic environment gives an average harvest rate less than h_{max}.

Theorem 4.1. *Consider h_{av} to be the average of the maximum harvesting levels in Eq. (4.1). Then*

$$h_{av} := \frac{1}{p}\sum_{j=0}^{p-1} h_j < h_{max} := \frac{(\sqrt{\mu}-1)^2}{\mu-1}k_{av}.$$

PROOF: If Eq. (4.1) has no periodic solution, then no population persists. So, let $\{x_j\}_0^{p-1}$ be a periodic solution of period p (not necessarily minimal). Now, use the same argument as in the proof of Theorem 2.1 to obtain the result. □

Despite the inferiority of h_{av} as shown in Theorem 4.1, one cannot underestimate the flexibility of periodic harvesting in terms of harvesting efforts and the effect on populations. Let $0 < \beta \leq k_j$ for all $0 \leq j < p$ and take

$$h_j = \frac{\beta(\mu-1)(k_j-\beta)}{k_j + (\mu-1)\beta},$$

then $\bar{x} = \beta$ is an equilibrium of Eq. (4.1). Furthermore, when β is unstable, i.e.,

$$\prod_{j=0}^{p-1}(1 + \frac{\mu-1}{k_j}\beta) \leq \mu^{\frac{p}{2}},$$

then $[\beta, \infty)$ is the persistent set, which gives us the advantage of controlling the persistent set for the benefit of low level populations.

Theorems 2.1 and 4.1 along with the results of [3] prove that in order to maximize harvesting, when given a choice of environment and type of harvesting, constant harvesting in constant environment is superior. Suppose we are given a choice between two options: (1) periodically harvesting in a constant capacity environment and (2) constantly harvesting in a periodic environment. The next theorem asserts that option (1) can be better if done carefully.

Theorem 4.2. *Let $h_{\max}$ be the maximum harvesting level that can be achieved with periodic carrying capacity $\{k_0, k_1, \ldots, k_{p-1}\}$. We can find harvesting quotas $h_0, h_1, \ldots, h_{p-1}$ in a constant environment with $k_{av} = \frac{1}{p}\sum k_j$ such that $\frac{1}{p}\sum h_j > h_{\max}$.*

PROOF: Take the maximum harvesting level h^* in a constant environment with k_{av}, then $h^* > h_{\max}$ by Theorem 2.1. Now take $h_0, h_1, \ldots, h_{p-1} \in [h^* - \epsilon, h^* + \epsilon]$ for sufficiently small ϵ to achieve the required task. □

4.2 Resonance and Attenuance

It is well known [13, 14] that populations governed by the periodic Beverton-Holt model

$$x_{n+1} = \frac{\mu k_n x_n}{k_n + (\mu - 1)x_n} \tag{4.3}$$

exhibit attenuance, i.e., the average of the stable cycle is less than the stable equilibrium in the deterministic Beverton-Holt model with carrying capacity equals the average of the carrying capacities in Eq. (4.3). Also, AlSharawi and Rhouma [3] found that periodic harvesting in a deterministic environment

$$x_{n+1} = \frac{\mu k x_n}{k + (\mu - 1)x_n} - h_n \tag{4.4}$$

forces populations governed by the Beverton-Holt model to attenuate. This discussion motivates us to discuss whether populations governed by Eq. (4.1) exhibit attenuance too. Indeed, our next theorem shows that the Cushing-Henson Conjecture [13, 14, 16, 18, 8] is valid for Eq. (4.1).

Theorem 4.3. *Populations governed by Eq. (4.1) exhibit attenuance.*

To simplify the proof, let us give some simple facts. For constant harvesting in a constant environment with $k = k_{av} = \sum_{j=0}^{p-1} k_j$, simple computations show that the stable equilibrium $\bar{x}_2$ of

$$x_{n+1} = \frac{\mu k_{av} x_n}{k_{av} + (\mu - 1)x_n} - h_{av} \tag{4.5}$$

satisfies the inequality

$$\frac{\sqrt{\mu} - 1}{\mu - 1} k_{av} \leq \bar{x}_2 < k_{av}. \tag{4.6}$$

The next lemma [24] is a simple generalization of Jensen's inequality.

Lemma 4.1. *Let $g : \mathbb{R}^+ \to \mathbb{R}$ be a strictly concave function, and let $f : {\mathbb{R}^+}^2 \to \mathbb{R}$ be defined as $f(x,k) = kg(\frac{x}{k})$, then*

$$\sum_{j=1}^{n} f(x_j, k_j) \leq f\left(\sum_{j=1}^{n} x_j, \sum_{j=1}^{n} k_j\right).$$

Now, we are ready to prove Theorem 4.3.

Proof of Theorem 4.3. If $\mathrm{tr}\,(\mathcal{B}_p) < 2\mu^{\frac{p}{2}} \prod_{j=0}^{p-1} k_j$, where $\mathcal{B}_p$ as defined in Eq. (2.4) and B_j as defined in Eq. (4.2), then no population will persist. So, we assume $\mathrm{tr}\,(\mathcal{B}_p) \geq 2\mu^{\frac{p}{2}} \prod_{j=0}^{p-1} k_j$ and consider x_{av} to be the average of the stable p-cycle (the period is not necessarily minimal) of Eq. (4.1). Also, let $\bar{x}_2$ be the stable equilibrium of Eq. (4.5). From Eq. (4.5), we obtain

$$h_{av} = \frac{\bar{x}_2(\mu - 1)(k_{av} - \bar{x}_2)}{k_{av} + (\mu - 1)\bar{x}_2},$$

and from Eq. (4.1), we obtain

$$h_{av} = \frac{1}{p}\sum_{j=0}^{p-1} \frac{x_j(\mu-1)(k_j - x_j)}{k_j + (\mu-1)x_j}.$$

Thus,

$$\frac{\bar{x}_2(\mu-1)(k_{av} - \bar{x}_2)}{k_{av} + (\mu-1)\bar{x}_2} = \frac{1}{p}\sum_{j=0}^{p-1} \frac{x_j(\mu-1)(k_j - x_j)}{k_j + (\mu-1)x_j},$$

and from Lemma 4.1,

$$\frac{\bar{x}_2(k_{av} - \bar{x}_2)}{k_{av} + (\mu-1)\bar{x}_2} \leq \frac{x_{av}(k_{av} - x_{av})}{k_{av} + (\mu-1)x_{av}}.$$

Now, use Inequality (4.6) and the fact that $h(t) := \frac{t(k_{av}-t)}{k_{av}+(\mu-1)t}$ is decreasing on the interval $[\frac{\sqrt{\mu}-1}{\mu-1}k_{av}, \infty)$ to obtain $x_{av} \leq \bar{x}_2$. □

4.3 The case $p = 2$

Let us focus on Eq. (4.1) with $p = 2$.

Lemma 4.2. *Consider periodic harvesting in a periodic environment with $p = 2$. Then*

$$h_j < \frac{(\mu-1)k_0k_1}{\mu k_{j+1} + k_j} < k_j.$$

PROOF: Solve $\operatorname{tr}(B_1B_0) - 2\mu k_0k_1 = 0$ for h_j to obtain

$$(\mu-1)k_0k_1 = h_0k_0 + h_1k_1 + \mu(h_0k_1 + h_1k_0) + h_0h_1(\mu-1). \tag{4.7}$$

In particular, if both h_0 and h_1 are non-negative then

$$h_0 < \frac{(\mu-1)k_0k_1}{k_0 + \mu k_1} \leq k_0 \qquad \text{and} \qquad h_1 < \frac{(\mu-1)k_0k_1}{k_1 + \mu k_0} \leq k_1.$$

□

Theorem 4.4. *Consider Eq. (4.1) with $p = 2$.*

(i) If $k_1 \geq \sqrt{\mu}k_0$, then $h_0 = 0$ and $h_1 = \dfrac{(\mu-1)k_0k_1}{k_0\mu + k_1}$ give the maximum harvesting average, and the 2-cycle is

$$\{\bar{x}_0, \bar{x}_1\} = \left\{\frac{k_1k_0}{k_0\mu + k_1}, \frac{k_0k_1}{k_1 + k_0}\right\}.$$

(ii) If $k_0 < \sqrt{\mu}k_1 < \mu k_0$, then

$$h_0 = \frac{k_0\sqrt{\mu} - k_1}{\sqrt{\mu} + 1} \quad \textit{and} \quad h_1 = \frac{k_1\sqrt{\mu} - k_0}{\sqrt{\mu} + 1}$$

give the maximum harvesting average, and the 2-cycle is

$$\{\bar{x}_0, \bar{x}_1\} = \left\{\frac{k_0}{\sqrt{\mu} + 1}, \frac{k_1}{\sqrt{\mu} + 1}\right\}.$$

(iii) If $\sqrt{\mu}k_1 \leq k_0$, then $h_1 = 0$ and $h_0 = \dfrac{(\mu-1)k_0k_1}{k_1\mu + k_0}$ give the maximum harvesting average, and, the 2-cycle is

$$\{\bar{x}_0, \bar{x}_1\} = \left\{ \frac{k_1k_0}{k_0+k_1}, \frac{k_0k_1}{\mu k_1 + k_0} \right\}.$$

Furthermore, the persistent set in each case is $[\bar{x}_0, \infty)$.

PROOF: To prove (ii), use Lagrange multipliers to maximize the average of h_0 and h_1 subject to the constraint $\operatorname{tr}(B_1B_0) = 2\mu k_0k_1$, then use the known values of h_0 and h_1 to find the 2-cycle. The values of h_0 and h_1 in (i) follow from (ii) and the extra constraints on h_0 and h_1 as given in Lemma 4.2, then use the known values of h_0 and h_1 to find the 2-cycle. (iii) follows from (i) by swapping the order of k_0 and k_1. □

Next, we make comparison between the harvesting strategies.

Theorem 4.5. *Consider $p = 2$ and assume the initial population is sufficiently large. Periodic harvesting in a periodic environment gives larger harvesting average compared to constant harvesting in a periodic environment.*

PROOF: Consider $h_0 = h_1 = h_{\max}$ and solve $\operatorname{tr}(B_1B_0) = 2\mu k_0k_1$ for $h_{\max}$ to find

$$h_{\max} = \frac{k_1+k_0}{2}\frac{\mu+1}{\mu-1} - \frac{\sqrt{(\mu+1)^2(k_1-k_0)^2 + 16\mu k_0k_1}}{2(\mu-1)}.$$

Now, compare $h_{\max}$ with the average of h_0 and h_1 from Theorem 4.4. If $k_1 \geq \sqrt{\mu}k_0$, then $h_{av} = \frac{(\mu-1)k_0k_1}{2(k_0\mu+k1)}$ and $h_{av} - h_{\max} = 0$ when

$$k_1 = \frac{1}{4}(-(\mu-1) - \sqrt{(\mu-1)^2+16\mu})k_0, 0, \frac{1}{4}(-(\mu-1) + \sqrt{(\mu-1)^2+16\mu})k_0.$$

However, since

$$\frac{1}{4}(-(\mu-1) + \sqrt{(\mu-1)^2+16\mu})k_0 < \sqrt{\mu}k_0,$$

then $h_{av} - h_{\max}$ does not change sign for all $k_1 > \sqrt{\mu}k_0$. Furthermore, fixed values of μ, k_0, k_1 show that $h_{av} - h_{\max} > 0$. If $k_0 < \sqrt{\mu}k_1 < \mu k_0$, then $h_{av} = \frac{k_0+k_1}{2}\frac{(\sqrt{\mu}-1)}{\sqrt{\mu}+1}$, and $h_{av} - h_{\max} = 0$ if and only if $k_0 = k_1$. Assuming $k_0 \neq k_1$, we obtain $h_{av} - h_{\max} > 0$. □

Now, let us present a detailed comparison in the following illustrative examples:

Example 4.1. *Consider*

$$x_{n+1} = \frac{\mu x_n}{1+(\mu-1)x_n} - h, \tag{4.8}$$

$$y_{n+1} = \frac{\mu(1+(-1)^nk)y_n}{(1+(-1)^nk)+(\mu-1)y_n} - h, \qquad 0<k<1 \tag{4.9}$$

$$z_{n+1} = \frac{\mu(1+(-1)^nk)z_n}{(1+(-1)^nk)+(\mu-1)z_n} - h_n, \qquad 0<k<1. \tag{4.10}$$

The first equation is for constant harvesting in constant environment, Eq. (4.9) is for constant harvesting in periodic environment and Eq.(4.10) is for periodic harvesting in periodic environment. Notice that we are taking $k = 1$ in (4.8), while in both (4.9) and (4.10) and for comparison reasons we assumed that the carrying capacities alternate periodically between the values $k_0 := (1+k)$ and $k_1 := (1-k)$ to obtain the average $k_{av} = 1$. Let h_{cc}, h_{pc} and h_{pp} be respectively the maximal harvesting levels for equations (4.8), (4.9) and (4.10). Straightforward computations give

$$h_{pc} \leq h_{pp} \leq h_{cc}, \tag{4.11}$$

where

$$\begin{aligned} h_{pc} &= \frac{(\mu+1) - \sqrt{(\mu-1)^2k^2+4\mu}}{\mu-1}, && (4.12)\\ h_{cc} &= \frac{(\sqrt{\mu}-1)^2}{\mu-1}, && (4.13)\\ h_{pp} &= \begin{cases} h_{cc} & \text{if } k \leq \frac{(\sqrt{\mu}-1)^2}{\mu-1} \\ \frac{(\mu-1)(1-k^2)}{2[(\mu+1)+k(1-\mu)]} & \text{if } \frac{(\sqrt{\mu}-1)^2}{\mu-1} < k < 1. \end{cases} && (4.14) \end{aligned}$$

Example 4.2. *In each of the following cases, consider $p = 2$:*

(i) Consider periodic harvesting in a periodic environment with $\mu = 4, k_0 = 3, k_1 = 5, h_0 = \frac{1}{3}$ and $h_1 = \frac{7}{3}$. Then

- *The average harvesting is $\frac{1}{2}(h_0 + h_1) = \frac{4}{3}$.*
- *The 2-cycle is $\{\bar{x}_0, \bar{x}_1\} = \{1, \frac{5}{3}\}$, which has an average of $\frac{4}{3}$.*
- *The persistent set is $[\bar{x}_0, \infty) = [1, \infty)$.*

(ii) Consider constant harvesting in a periodic environment with $\mu = 4, k_0 = 3, k_1 = 5$. Then

- *The average harvesting is $h_{\max} = \frac{1}{3}(20 - \sqrt{265}) \approx 1.240$.*
- *The 2-cycle is*

$$\{\bar{x}_0, \bar{x}_1\} = \left\{ \frac{-5}{8} + \frac{\sqrt{265}}{8}, \frac{-55}{24} + \frac{5\sqrt{265}}{24} \right\},$$

  which has an average of $\frac{-35}{24} + \frac{\sqrt{265}}{6} \approx 1.255$.
- *The persistent set is $[\bar{x}_0, \infty) \approx [1.410, \infty)$.*

5 Conclusion and Discussion

In a previous paper [3], we have established that for the deterministic Beverton-Holt model, constant harvesting is superior to both periodic and conditional harvesting when the maximum sustainable yield is taken as the management objective, and when the initial population is sufficiently large. In this paper, we obtained

- Constant harvesting in a constant environment is "better" than constant harvesting in a periodic environment (Theorem 2.1).
- Constant harvesting in a constant environment is "better" than periodic harvesting in a periodic environment (Theorem 4.1). However, at least in the case $p = 2$ and for some range of the parameters, careful harvesting can lead to the same yield as the optimal constant harvesting.
- Periodic harvesting in a periodic environment is "better" than constant harvesting in a periodic environment.

Finally, this study left us with few questions that deserve further investigations.

Question 1: Fix a set of carrying capacities $\{k_0, k_1, \ldots, k_{p-1}\}$, and consider all permutations of $(k_0, k_1, \ldots, k_{p-1})$ in Eq. (3.1). According to the Theorem 3.1, we obtain $\frac{1}{2}(p-1)!$ values for $h_{\max}$, and Theorem 3.2 characterizes those values for $p = 2, 3, 4$ and 5. Complete the characterization for general p.

Question 2: Consider Eq. (4.1) and let $H := \{h_0, h_1, \ldots, h_{p-1}\}$ be a set of harvesting quotas that give a nonempty persistent set. Which permutation of H would enlarge the persistent set?

Question 3: Generalize the results of this study to the case where the inheritance growth rate μ is nonconstant.

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