

Research Article

The Discrete Beverton-Holt Model with Periodic Harvesting in a Periodically Fluctuating Environment

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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.

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 [1]. 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 carrying business as usual. 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, different types of bifurcations, catastrophe, and even chaotic behavior [2–7]. Optimal harvesting for single species has been studied by several authors from different points of view; see for example [8–10] and the references therein. Recently, Braverman and Mamadani [11] considered both autonomous and nonautonomous 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 [12] and Xu et al. [13]. For single species, Ludwig [12] studied models with random fluctuations and found that constant effort harvesting does worse than other harvesting strategies. Xu et al. [13] 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 [14], 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 [15]. The stochastic Beverton-Holt equation with constant and proportional harvesting was studied in [16]. A special type of periodic impulsive harvesting in relation with seasonal environment was also studied in [17]. In [18], 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 [19].

This paper is a continuation of [19] 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

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

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 [20]. 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 and the basin of attraction of the stable periodic solution. In Section 4, we address different aspects of constant yield harvesting in periodic environment, then we focus on periodic harvesting in periodic environments and its effect on population's resonance/attenuance. We make a comparison with other harvesting strategies and give a full discussion when $p = 2$. Finally, we close the paper with a brief conclusion and a few questions that are worth further investigation.

2. Preliminary

In this section, we give a preliminary result that is necessary in our consequent analysis. Assume we have constant harvesting on (1.1) with periodically fluctuating carrying capacities, that is,

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

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 $\mu > 1$. Next, 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 (2.1) take the form

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

For each $j = 0, \dots, p - 1$, 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

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

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 [19].

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

- (i) *If $\text{tr}(\mathcal{B}_p) > 2\mu^{p/2} \prod_{j=0}^{p-1} k_j$, then there exist two p -cycles; one of them is stable and the other is unstable.*
- (ii) *If $\text{tr}(\mathcal{B}_p) = 2\mu^{p/2} \prod_{j=0}^{p-1} k_j$, then exactly one semistable p -cycle exists.*
- (iii) *If $\text{tr}(\mathcal{B}_p) < 2\mu^{p/2} \prod_{j=0}^{p-1} k_j$, then there are no periodic solutions and consequently, no population persists.*

Proof. It follows along the same lines as [19, Proof of Theorem 3.3]. Nevertheless, it is enough to observe that the cycles depend on the monotonically increasing function $F_p(x)$ in (2.2). $F_p(x)$ has two fixed points if and only if the eigenvalues of the matrix \mathcal{B}_p in (2.4) are distinct real numbers. The eigenvalues of \mathcal{B}_p are given by

$$\frac{1}{2} \operatorname{tr}(\mathcal{B}_p) \pm \frac{1}{2} \sqrt{(\operatorname{tr}(\mathcal{B}_p))^2 - 4 \det(\mathcal{B}_p)}, \quad (2.5)$$

and the radicand gives the conditions in (i), (ii), and (iii). If $\bar{y}_0 \leq \bar{y}_1$ are the two fixed points of F_p , then

$$\mathcal{O}(\bar{y}_j) = \{\bar{y}_j, F_1(\bar{y}_j), F_2(\bar{y}_j), \dots, F_{p-1}(\bar{y}_j)\}, \quad j = 0, 1, \quad (2.6)$$

are the two p -cycles of (2.1). Furthermore, since $F_p(x)$ is strictly increasing, then the positive equilibrium \bar{y}_0 is unstable and \bar{y}_1 is stable. When $\bar{y}_0 = \bar{y}_1$ at $\operatorname{tr}(\mathcal{B}_p) = 2\mu^{p/2} \prod_{j=0}^{p-1} k_j$, we obtain semistability (stability from above only). Because the maps f_j , $0 \leq j \leq p-1$ are continuous, then the cycles of (2.1) inherit the stability of \bar{y}_0 and \bar{y}_1 under the monotonic map F_p . Finally, when F_p has no fixed points, then we have a monotonically increasing function below $y = x$ and obviously, orbits go negative in finite time. \square

Proposition 2.1 shows that a constraint on h is necessary to assure the long-term survival of a population governed by (2.1). The harvesting level reaches its maximum h_{\max} when the p -cycle becomes semistable. Thus, we proceed with the assumption that $0 \leq h \leq h_{\max}$, and h_{\max} is the smallest positive solution of the equation $\operatorname{tr}(\mathcal{B}_p) = 2\mu^{p/2} \prod_{j=0}^{p-1} k_j$.

3. Harvesting Levels and the Basin of Attraction

It is well known [21, 22] that for $h = 0$, system (2.1) has a globally asymptotically stable p -cycle, that is, the basin of attraction of the p -cycle is \mathbb{R}^+ . In this section, we consider (2.1) with $0 < h \leq h_{\max}$ and investigate the basin of attraction of the stable/semistable p -cycle. But first, we give a few necessary definitions. A solution of (2.1) is called persistent if the corresponding initial population survives indefinitely. Here, it is worth emphasizing that although one can start iterating (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 $\mathfrak{D} := \{x : x \in \mathbb{R}^+\}$ is persistent if each solution of (2.1) with $x_0 \in \mathfrak{D}$ is persistent. We refer those who are interested in reading more about persistence and its significance to [23, 24]. At a harvesting level h , let \mathfrak{D}_h be the largest persistent set, which we simply call the persistent set. Obviously, when $h = 0$, $\mathfrak{D}_0 = [0, \infty)$, and \mathfrak{D}_h is empty when $h > h_{\max}$. Thus, a persistent set must contain the basin of attraction of the stable p -cycle assured by Proposition 2.1.

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

Proof. Since $h < h_{\max}$, then the map $F_p(x)$ defined in (2.2) has two fixed points, say $\bar{x}_{0,l}$ and $\bar{x}_{0,r}$, where $\bar{x}_{0,l} \leq \bar{x}_{0,r}$. Now, the other elements of the unstable cycle are given by $\bar{x}_{1,l} = f_0(\bar{x}_{0,l}), \bar{x}_{2,l} = f_1(f_0(\bar{x}_{0,l})) = f_1(\bar{x}_{1,l}), \dots$. Let $x_0 \geq \bar{x}_{0,l}$. From the monotonicity of the maps $f_j, j = 0, \dots, p-1$, we obtain $x_{n+1} \geq \bar{x}_{n \bmod p,l} > 0$ for all $n \in \mathbb{N}$. Thus $[\bar{x}_{0,l}, \infty) \subseteq \mathfrak{D}_h$. 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 $n, x_{np+1} = F_{p-1}^n(x_0) < 0$, which completes the proof. \square

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

$$[\max\{s_{l,j}, j = 0, \dots, p-1\}, \infty) \subseteq \mathfrak{D}_h, \quad \mathfrak{D}_h \subseteq [\min\{s_{l,j-1}, j = 0, \dots, p-1\}, \infty). \quad (3.1)$$

Proof. Since $h \leq (\sqrt{\mu} - 1)^2 k_j / (\mu - 1)$ for each j , then each map f_j has two fixed points $s_{l,j} \leq k / (\sqrt{\mu} + 1) \leq s_{r,j}$. Now, trace the iterates of (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 4.2 shows that we can achieve a maximum harvesting level by taking a constant carrying capacity, that is, $p = 1$. 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

$$x_{n+1} = f_{j_n}(x_n) := \frac{k_{j_n} \mu x_n}{k_{j_n} + (\mu - 1)x_n} - h, \quad n \in \mathbb{N}, \quad (3.2)$$

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

Theorem 3.3. *Fix a set of carrying capacities $\{k_0, k_1, \dots, k_{p-1}\}$. All equations of the form (3.2) with permutations $(j_0, j_1, \dots, j_{p-1})$ in the dihedral group of order p give the same maximum constant harvesting level.*

Proof. The maximum harvesting level is the smallest positive solution of the equation

$$\text{tr}(B_{j_p} B_{j_{p-1}} \cdots B_{j_0}) - 2\mu^{p/2} k_0 k_1 \cdots k_{p-1} = 0. \quad (3.3)$$

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

$$\text{tr}(B_{j_{p-1}} B_{j_{p-2}} \cdots B_{j_0}) = \text{tr}(B_{j_0} B_{j_1} \cdots B_{j_{p-1}}). \quad (3.4)$$

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

$$A := \begin{bmatrix} 1 & 0 \\ -h & \mu \end{bmatrix}, \quad C := \begin{bmatrix} 0 & 1 \\ 0 & -h \end{bmatrix}. \quad (3.5)$$

By simple induction, we can show that

$$A^n = \begin{bmatrix} 1 & 0 \\ -h \frac{(\mu^{n+1} - 1)}{\mu - 1} & \mu^n \end{bmatrix}, \quad C^n = (-h)^{n-1}C. \quad (3.6)$$

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

$$\begin{aligned} \operatorname{tr}(B_{j_{p-1}}B_{j_{p-2}} \cdots B_{j_0}) &= \sum_{S \in \mathcal{P}} (\mu - 1)^{p-|S|} \prod_{i \in S} k_{j_i} \operatorname{tr}(D(S)), \\ \operatorname{tr}(B_{j_0}B_{j_1} \cdots B_{j_{p-1}}) &= \sum_{S \in \mathcal{P}} (\mu - 1)^{p-|S|} \prod_{i \in S} k_{j_i} \operatorname{tr}(\widehat{D}(S)), \end{aligned} \quad (3.7)$$

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

$$\begin{aligned} D(S) &= D_{p-1}(S)D_{p-2}(S) \cdots D_1(S)D_0(S), \\ \widehat{D}(S) &= D_0(S)D_1(S) \cdots D_{p-2}(S)D_{p-1}(S), \\ D_j(S) &= \begin{cases} A & \text{if } j \in S, \\ C & \text{otherwise.} \end{cases} \end{aligned} \quad (3.8)$$

Now, proving (3.4) is equivalent to proving that

$$\operatorname{tr}(D_{p-1}(S)D_{p-2}(S) \cdots D_0(S)) = \operatorname{tr}(D_0(S)D_1(S) \cdots D_{p-1}(S)). \quad (3.9)$$

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

$$\operatorname{tr}(D(S)) = \operatorname{tr}(A^{\alpha_1}C^{\beta_1}A^{\alpha_2}C^{\beta_2} \cdots A^{\alpha_m}C^{\beta_m}) = (-h)^{-m+\sum \beta_i} \operatorname{tr}(A^{\alpha_1}CA^{\alpha_2}C \cdots A^{\alpha_m}C) \quad (3.10)$$

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

$$A^{\alpha_i} C = \begin{bmatrix} 0 & 1 \\ 0 & \gamma_{\alpha_i} \end{bmatrix}, \quad \gamma_{\alpha_i} = -\frac{(\mu^{\alpha_i+1} - 1)h}{\mu - 1}, \tag{3.11}$$

then

$$\text{tr}(D(S)) = (-h)^{-m+\sum \beta_i} \prod_{i=1}^m \gamma_{\alpha_i}. \tag{3.12}$$

On the other hand,

$$\begin{aligned} \text{tr}(\widehat{D}(S)) &= \text{tr}(C^{\beta_m} A^{\alpha_m} \dots C^{\beta_2} A^{\alpha_2} C^{\beta_1} A^{\alpha_1}) \\ &= \text{tr}(A^{\alpha_m} \dots C^{\beta_2} A^{\alpha_2} C^{\beta_1} A^{\alpha_1} C^{\beta_m}) \\ &= (-h)^{-m+\sum \beta_i} \text{tr}(A^{\alpha_m} C \dots A^{\alpha_2} C A^{\alpha_1} C) \\ &= (-h)^{-m+\sum \beta_i} \prod_{i=1}^m \gamma_{\alpha_i}, \end{aligned} \tag{3.13}$$

which completes the desired proof. □

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

$$\begin{aligned} \text{tr}(\mathcal{B}_2) &= (1 - \mu)^2 h^2 - (\mu - 1)(\mu + 1)(k_0 + k_1)h + k_1 k_0 (\mu^2 + 1), \\ \text{tr}(\mathcal{B}_3) &= -(\mu - 1)^3 (h)^3 + (\mu + 1)(\mu - 1)^2 h^2 \left(\sum_{j=0}^2 k_j \right) \\ &\quad - h \left((\mu^3 - 1) \sum_{i=0}^1 \sum_{j=i+1}^2 k_i k_j \right) + k_2 k_1 k_0 (\mu^3 + 1), \\ \text{tr}(\mathcal{B}_4) &= (\mu - 1)^4 h^4 - (\mu + 1)(\mu - 1)^3 h^3 \left(\sum_{j=0}^3 k_j \right) \\ &\quad + (\mu - 1)^2 h^2 \left(\mu(k_0 k_2 + k_1 k_3) + (\mu^2 + \mu + 1) \sum_{i=0}^2 \sum_{j=i+1}^3 k_j k_i \right) \\ &\quad - (\mu^4 - 1) k_0 k_1 k_2 k_3 h \left(\sum_{j=0}^3 \frac{1}{k_j} \right) + (\mu^4 + 1) k_0 k_1 k_2 k_3. \end{aligned} \tag{3.14}$$

Example 3.4. (i) Consider the case $p = 2, k_0 = 1, k_1 = 4$, and $\mu = 4$. Then the value of $h_{\max} = 1/6(25 - \sqrt{481})$ and the semistable 2-cycle is $\{\bar{y}_0 = 1/30(\sqrt{481} - 1), \bar{y}_1 = 2/15(\sqrt{481} - 19)\}$ with the interval $[1/30(\sqrt{481} - 1), \infty)$ 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 $[2/15(\sqrt{481} - 19), \infty)$. 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 $\text{tr}(\mathcal{B}_4)$ can only take three possible values. For each of these values, there corresponds a value of h_{\max} . For instance, if

$$\{k_j\} = \left\{ j + 10 \left(1 + (-1)^j \right) : j = 0, 1, 2, 3 \right\}, \quad (3.15)$$

then $(k_0, k_1, k_2, k_3) = (20, 1, 22, 3), (3, 22, 1, 20)$ and their cyclic permutations 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 permutations 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 permutations 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 3.5. *Consider (3.2) and assume the initial population is sufficiently large. Without loss of generality, let $k_0 \leq k_1 \leq \dots \leq k_{p-1}$. 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 permutations 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 permutations give the smallest.

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

$$\text{tr}(B_{j_{p-1}} B_{j_{p-2}} \cdots B_{j_1} B_{j_0}) = 2\sqrt{\det(B_{j_{p-1}} B_{j_{p-2}} \cdots B_{j_1} B_{j_0})} = 2\mu^{p/2} \prod_{i=0}^{p-1} k_i, \quad (3.16)$$

then we need to investigate the minimum positive value of h that satisfies this equation. (i) follows straight from the expressions of $\text{tr}(\mathcal{B}_2)$ and $\text{tr}(\mathcal{B}_3)$. 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 3.3 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

$$\begin{aligned} q_1(h) &:= \text{tr}(B_3 B_2 B_0 B_1) - 2\mu^2 k_3 k_2 k_1 k_0, \\ q_2(h) &:= \text{tr}(B_3 B_2 B_1 B_0) - 2\mu^2 k_3 k_2 k_1 k_0, \\ q_3(h) &:= \text{tr}(B_3 B_0 B_2 B_1) - 2\mu^2 k_3 k_2 k_1 k_0, \end{aligned} \quad (3.17)$$

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

$$\begin{aligned} q_3(h) &= q_2(h) + \mu(\mu - 1)^2 (k_1 - k_2)(k_0 - k_3)h^2, \\ q_3(h) &= q_1(h) + \mu(\mu - 1)^2 (k_1 - k_3)(k_0 - k_2)h^2, \\ q_1(h) &= q_2(h) + \mu(\mu - 1)^2 (k_3 - k_2)(k_0 - k_1)h^2. \end{aligned} \quad (3.18)$$

Now, $q_1(h_{\max 2}) \leq 0$ implies that $h_{\max 1} \leq h_{\max 2}$, $q_1(h_{\max 3}) \leq 0$ implies that $h_{\max 1} \leq h_{\max 3}$ and $q_2(h_{\max 3}) \leq 0$ implies that $h_{\max 2} \leq h_{\max 3}$. 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. \square

4. Periodic Harvesting in a Periodic Environment

In this section, we consider

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

Observe that if $h_n = h$ for all n , then we have the constant yield harvesting. Thus we discuss the constant yield harvesting first followed by the more general periodic case, then we discuss resonance and attenuation. Finally, for the sake of concreteness, we focus on the specific case $p = 2$.

4.1. Constant Yield Harvesting in a Periodic Environment

We force $h_n = h$ in (4.1) to obtain (2.1). Observe that $f_j(x)$ is asymptotic to $\mu k_j / \mu - 1$. So, it is obvious that $0 \leq h \leq h_{\max} < \min\{(\mu/\mu - 1)k_j, j = 0, 1, \dots, p - 1\}$, 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 4.1. *Consider (2.1), then*

$$h_{\max} < \min \left\{ \left(\sum_{j=0}^{p-1} \mu^j \right) \left(\sum_{j=0}^{p-1} \frac{\mu^j}{k_{j+i \bmod p}} \right)^{-1}, i = 0, 1, \dots, p - 1 \right\}. \tag{4.2}$$

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

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 [21, 22, 25, 26]. This suggests that periodic environment has a negative impact on the maximum harvesting level. Indeed, we have the following result.

Theorem 4.2. *Consider (2.1); then the maximum harvesting level h_{\max} in a periodic environment is less than the maximum harvesting level in a constant environment with $k = k_{av} := 1/p \sum_{j=0}^{p-1} k_j$.*

Proof. Let $\{\bar{x}_0, \bar{x}_1, \dots, \bar{x}_{p-1}\}$ be the semistable p -cycle assured at the maximum harvesting level h_{\max} . From (2.1), we obtain

$$\sum_{j=0}^{p-1} x_j = -ph_{\max} + \sum_{j=0}^{p-1} \frac{k_j \mu x_j}{k_j + (\mu - 1)x_j} \tag{4.3}$$

and thus

$$h_{\max} = \frac{1}{p} \sum_{j=0}^{p-1} \left(\frac{k_j \mu x_j}{k_j + (\mu - 1)x_j} - x_j \right). \tag{4.4}$$

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

$$h_{\max} < \frac{1}{p} \frac{(\sqrt{\mu} - 1)^2}{(\mu - 1)} \sum_{j=0}^{p-1} k_j = \frac{(\sqrt{\mu} - 1)^2}{(\mu - 1)} k_{av}. \tag{4.5}$$

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

4.2. The General Case

By considering the matrix of (2.3) to be

$$B_j := \begin{bmatrix} k_j & \mu - 1 \\ -h_j k_j & \mu k_j - h_j(\mu - 1) \end{bmatrix}, \tag{4.6}$$

Proposition 2.1 continues to hold with the exception that cycles period may not be minimal, that is, 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

$$k_0 = \frac{1}{2}(9 + 3\sqrt{17}), \quad k_1 = 9, \quad k_3 = \frac{1}{4}(15 + 3\sqrt{57}), \quad k_4 = \frac{1}{5}(3 + 2\sqrt{21}), \quad h_j = \frac{3(k_j - 1)}{k_j + 3}. \tag{4.7}$$

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 [27, 28].

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

Theorem 4.3. Consider h_{av} to be the average of the maximum harvesting levels in (4.1). Then

$$h_{av} := \frac{1}{p} \sum_{j=0}^{p-1} h_j < h_{max} := \frac{(\sqrt{\mu} - 1)^2}{\mu - 1} k_{av}. \tag{4.8}$$

Proof. If (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 4.2 to obtain the result. \square

Despite the inferiority of h_{av} as shown in Theorem 4.3, 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

$$h_j = \frac{\beta(\mu - 1)(k_j - \beta)}{k_j + (\mu - 1)\beta}; \tag{4.9}$$

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

$$\prod_{j=0}^{p-1} \left(1 + \frac{\mu - 1}{k_j} \beta \right) \leq \mu^{p/2}, \tag{4.10}$$

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 4.2 and 4.3 along with the results of [19] 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 4.4. *Let h_{\max} be the maximum harvesting level that can be achieved with periodic carrying capacity $\{k_0, k_1, \dots, k_{p-1}\}$. We can find harvesting quotas h_0, h_1, \dots, h_{p-1} in a constant environment with $k_{av} = 1/p \sum k_j$ such that $1/p \sum h_j > h_{\max}$.*

Proof. Take the maximum harvesting level h^* in a constant environment with k_{av} , then $h^* > h_{\max}$ by Theorem 4.2. Now take $h_0, h_1, \dots, h_{p-1} \in [h^* - \epsilon, h^* + \epsilon]$ for sufficiently small ϵ to achieve the required task. \square

4.3. Resonance and Attenuance

It is well known [21, 25] that populations governed by the periodic Beverton-Holt model

$$x_{n+1} = \frac{\mu k_n x_n}{k_n + (\mu - 1)x_n} \quad (4.11)$$

exhibit attenuance, that is, the average of the stable cycle is less than the stable equilibrium in the deterministic Beverton-Holt model with carrying capacity equaling the average of the carrying capacities in (4.11). AlSharawi and Rhouma [19] also found that periodic harvesting in a deterministic environment

$$x_{n+1} = \frac{\mu k x_n}{k + (\mu - 1)x_n} - h_n \quad (4.12)$$

forces populations governed by the Beverton-Holt model to attenuate. This discussion motivates us to discuss whether populations governed by (4.1) exhibit attenuance too. Indeed, our next theorem shows that the Cushing-Henson Conjecture [21, 22, 25, 26, 29] is valid for (4.1).

Theorem 4.5. *Populations governed by (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 (or semistable) equilibrium \bar{x}_2 of

$$x_{n+1} = \frac{\mu k_{av} x_n}{k_{av} + (\mu - 1)x_n} - h_{av} \quad (4.13)$$

exists when $h_{av} \leq ((\sqrt{\mu} - 1)/(\sqrt{\mu} + 1))k_{av}$ and satisfies the inequality

$$\frac{\sqrt{\mu} - 1}{\mu - 1} k_{av} \leq \bar{x}_2 < k_{av}. \quad (4.14)$$

The next lemma [30] is a simple generalization of Jensen's inequality.

Lemma 4.6. Let $g : \mathbb{R}^+ \rightarrow \mathbb{R}$ be a strictly concave function, and let $f : \mathbb{R}^{+2} \rightarrow \mathbb{R}$ be defined as $f(x, k) = kg(x/k)$, then

$$\sum_{j=1}^n f(x_j, k_j) \leq f\left(\sum_{j=1}^n x_j, \sum_{j=1}^n k_j\right). \tag{4.15}$$

Now, we are ready to prove Theorem 4.5.

Proof of Theorem 4.5. If $\text{tr}(\mathcal{B}_p) < 2\mu^{p/2}\prod_{j=0}^{p-1}k_j$, where \mathcal{B}_p is as defined in (2.4) and B_j is as defined in (4.6), then no population will persist and thus, we have trivial attenuation. So, we assume $\text{tr}(\mathcal{B}_p) \geq 2\mu^{p/2}\prod_{j=0}^{p-1}k_j$ and consider x_{av} to be the average of the stable (or semistable) p -cycle (the period is not necessarily minimal) of (4.1). From (4.1), we obtain

$$h_{av} = \frac{1}{p} \sum_{j=0}^{p-1} \frac{x_j(\mu - 1)(k_j - x_j)}{k_j + (\mu - 1)x_j}. \tag{4.16}$$

Use Lemma 4.6 to obtain

$$h_{av} \leq \frac{(\mu - 1)x_{av}(k_{av} - x_{av})}{k_{av} + (\mu - 1)x_{av}} \leq \frac{\sqrt{\mu} - 1}{\sqrt{\mu} + 1}k_{av}. \tag{4.17}$$

Thus, \bar{x}_2 exists in (4.13) and

$$h_{av} = \frac{\bar{x}_2(\mu - 1)(k_{av} - \bar{x}_2)}{k_{av} + (\mu - 1)\bar{x}_2}. \tag{4.18}$$

From Inequality (4.17) and (4.18), we obtain

$$\frac{\bar{x}_2(k_{av} - \bar{x}_2)}{k_{av} + (\mu - 1)\bar{x}_2} \leq \frac{x_{av}(k_{av} - x_{av})}{k_{av} + (\mu - 1)x_{av}}. \tag{4.19}$$

Now, use Inequality (4.14) and the fact that $h(t) := t(k_{av} - t)/(k_{av} + (\mu - 1)t)$ is decreasing on the interval $[(\sqrt{\mu} - 1)/(\mu - 1)k_{av}, \infty)$ to obtain $x_{av} \leq \bar{x}_2$. \square

4.4. The Case $p = 2$

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

Lemma 4.7. Consider periodic harvesting in a periodic environment with $p = 2$. Then

$$h_j < \frac{(\mu - 1)k_0k_1}{\mu k_{j+1} + k_j} < k_j. \tag{4.20}$$

Proof. Solve $\text{tr}(B_1 B_0) - 2\mu k_0 k_1 = 0$ for h_j to obtain

$$(\mu - 1)k_0 k_1 = h_0 k_0 + h_1 k_1 + \mu(h_0 k_1 + h_1 k_0) + h_0 h_1 (\mu - 1). \quad (4.21)$$

In particular, if both h_0 and h_1 are nonnegative then

$$h_0 < \frac{(\mu - 1)k_0 k_1}{k_0 + \mu k_1} \leq k_0, \quad h_1 < \frac{(\mu - 1)k_0 k_1}{k_1 + \mu k_0} \leq k_1. \quad (4.22)$$

□

Theorem 4.8. Consider (4.1) with $p = 2$.

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

$$\{\bar{x}_0, \bar{x}_1\} = \left\{ \frac{k_1 k_0}{k_0 \mu + k_1}, \frac{k_0 k_1}{k_1 + k_0} \right\}. \quad (4.23)$$

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

$$h_0 = \frac{k_0 \sqrt{\mu} - k_1}{\sqrt{\mu} + 1}, \quad h_1 = \frac{k_1 \sqrt{\mu} - k_0}{\sqrt{\mu} + 1} \quad (4.24)$$

give the maximum harvesting average. Moreover, the 2-cycle is

$$\{\bar{x}_0, \bar{x}_1\} = \left\{ \frac{k_0}{\sqrt{\mu} + 1}, \frac{k_1}{\sqrt{\mu} + 1} \right\}. \quad (4.25)$$

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

$$\{\bar{x}_0, \bar{x}_1\} = \left\{ \frac{k_1 k_0}{k_0 + k_1}, \frac{k_0 k_1}{\mu k_1 + k_0} \right\}. \quad (4.26)$$

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 $\text{tr}(B_1 B_0) = 2\mu k_0 k_1$, 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 4.7, 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 4.9. 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 $\text{tr}(B_1 B_0) = 2\mu k_0 k_1$ for h_{\max} to find

$$h_{\max} = \frac{k_1 + k_0}{2} \frac{\mu + 1}{\mu - 1} - \frac{\sqrt{(\mu + 1)^2 (k_1 - k_0)^2 + 16\mu k_0 k_1}}{2(\mu - 1)}. \tag{4.27}$$

Now, compare h_{\max} with the average of h_0 and h_1 from Theorem 4.8. If $k_1 \geq \sqrt{\mu}k_0$, then $h_{av} = (\mu - 1)k_0 k_1 / 2(k_0\mu + k_1)$ and $h_{av} - h_{\max} = 0$ when

$$k_1 = \frac{1}{4} \left(-(\mu - 1) \pm \sqrt{(\mu - 1)^2 + 16\mu} \right) k_0, 0. \tag{4.28}$$

However, since

$$\frac{1}{4} \left(-(\mu - 1) + \sqrt{(\mu - 1)^2 + 16\mu} \right) k_0 < \sqrt{\mu}k_0, \tag{4.29}$$

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 $h_{av} = ((k_0 + k_1)/2) ((\sqrt{\mu} - 1)/(\sqrt{\mu} + 1))$, and $h_{av} - h_{\max} = 0$ if and only if $k_0 = k_1$. Assuming $k_0 \neq k_1$, we obtain $h_{av} - h_{\max} > 0$. \square

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

Example 4.10. Consider

$$x_{n+1} = \frac{\mu x_n}{1 + (\mu - 1)x_n} - h, \tag{4.30}$$

$$y_{n+1} = \frac{\mu(1 + (-1)^n k)y_n}{(1 + (-1)^n k) + (\mu - 1)y_n} - h, \quad 0 < k < 1, \tag{4.31}$$

$$z_{n+1} = \frac{\mu(1 + (-1)^n k)z_n}{(1 + (-1)^n k) + (\mu - 1)z_n} - h_n, \quad 0 < k < 1. \tag{4.32}$$

The first equation is for constant harvesting in a constant environment, (4.31) is for constant harvesting in a periodic environment, and (4.32) is for periodic harvesting in a periodic environment. Notice that we are taking $k = 1$ in (4.30), while in both (4.31) and (4.32) 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 (4.30), (4.31), and (4.32). Straightforward computations give

$$h_{pc} \leq h_{pp} \leq h_{cc}, \tag{4.33}$$

where

$$\begin{aligned}
 h_{pc} &= \frac{(\mu + 1) - \sqrt{(\mu - 1)^2 k^2 + 4\mu}}{\mu - 1}, \\
 h_{cc} &= \frac{(\sqrt{\mu} - 1)^2}{\mu - 1}, \\
 h_{pp} &= \begin{cases} h_{cc} & \text{if } k \leq \frac{(\sqrt{\mu} - 1)^2}{\mu - 1}, \\ \frac{(\mu - 1)(1 - k^2)}{2[(\mu + 1) + k(1 - \mu)]} & \text{if } \frac{(\sqrt{\mu} - 1)^2}{\mu - 1} < k < 1. \end{cases}
 \end{aligned} \tag{4.34}$$

Example 4.11. In each of the following cases, consider $p = 2$.

- (i) Consider periodic harvesting in a periodic environment with $\mu = 4, k_0 = 3, k_1 = 5, h_0 = 1/3$, and $h_1 = 7/3$. Then
 - (a) the average harvesting is $1/2(h_0 + h_1) = 4/3$;
 - (b) the 2-cycle is $\{\bar{x}_0, \bar{x}_1\} = \{1, 5/3\}$, which has an average of $4/3$;
 - (c) 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
 - (a) The average harvesting is $h_{\max} = 1/3(20 - \sqrt{265}) \approx 1.240$;
 - (b) The 2-cycle is

$$\{\bar{x}_0, \bar{x}_1\} = \left\{ \frac{-5}{8} + \frac{\sqrt{265}}{8}, \frac{-55}{24} + \frac{5\sqrt{265}}{24} \right\}, \tag{4.35}$$

which has an average of $(-35/24) + (\sqrt{265}/6) \approx 1.255$;

- (c) The persistent set is $[\bar{x}_0, \infty) \approx [1.410, \infty)$.

5. Conclusion and Discussion

In a previous paper [19], we have established that for the deterministic Beverton-Holt model, constant harvesting is superior to both periodic and conditional harvestings when the maximum sustainable yield is taken as the management objective, and when the initial population is sufficiently large. In this paper, we obtained the following.

- (i) Constant harvesting in a constant environment is “better” than constant harvesting in a periodic environment (Theorem 4.2).
- (ii) Constant harvesting in a constant environment is “better” than periodic harvesting in a periodic environment (Theorem 4.3). However, at least in the case $p = 2$ and for some range of the parameters, careful periodic harvesting can lead to the same yield as the optimal constant harvesting.
- (iii) 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 $\{k_0, k_1, \dots, k_{p-1}\}$, and consider all permutations of $(k_0, k_1, \dots, k_{p-1})$ in (3.2). According to the Theorem 3.3, we obtain $1/2(p-1)!$ values for h_{\max} , and Theorem 3.5 characterizes those values for $p = 2, 3, 4$, and 5. Complete the characterization for general p .

Question 2. Consider (4.1) and let $H := \{h_0, h_1, \dots, h_{p-1}\}$ 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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