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# Attenuant cycles in periodically forced discrete-time age-structured population models

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## Abstract

In discrete-time age-structured population models, a periodic environment is not always deleterious. We show that it is possible to have the average of the age class populations over an attracting cycle (in a periodic environment) not less than the average of the carrying capacities (in a corresponding constant environment). In our age-structured model, a periodic environment does not increase the average total biomass (no resonance). However, a periodic environment is disadvantageous for a population whenever there is no synchrony between the number of age classes and the period of the environment. As in periodically forced models without age-structure, we show that periodically forced age-structured population models support multiple attractors with complicated structures.

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## 1. Introduction

Temporal environmental fluctuations are common in nature and their causes are manifold. Periodic fluctuations, for example, are caused by annual or daily fluctuations in the physical environment [7,8]. Theoretical and experimental studies have focused on whether or not a population is adversely affected by a periodic environment relative to a constant

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environment. The controlled laboratory experiment of Jillson with a periodic food supply resulted in oscillations in population size of the flour beetle (*Tribolium*). In the alternating habitat, the total population numbers observed were more than twice those in the constant habitat even though the average flour volume was the same in both environments [6,8,16,21–26,45]. Henson and Cushing [25], Costantino et al. [6] and Henson et al. [23, 24] explained Jillson's observations. In [6,16,21–26], mathematical analysis and laboratory experiments were used to demonstrate that it is possible for a periodic environment to be advantageous for a population. Others have used either the logistic differential or difference equations (without age-structure) to show that a periodic environment is deleterious [4,5,8,37–39,41,48]. That is, the average of the resulting oscillations in the periodic environment is less than the average of the carrying capacity in a corresponding constant environment. Cushing and Henson obtained similar results for 2-periodic monotone models without age structure [8]. Kon [29,30], Kocic [27,28], Elaydi and Sacker [9–15] have since extended these results to include  $p$ -periodic Beverton–Holt population models without age-structure, where  $p > 2$ .

In this paper, we focus on the effects of periodic environments on age-structured populations. We replace the lumped one-population model in [3,8,11–15,27,29–31], with a  $p$ -periodically forced, age-structured, discrete-time population model of the form

$$x \rightarrow Ax,$$

where  $x$  is a population vector whose component  $x_i$  is the population in age class  $i$ ,  $A$  is a Leslie matrix with a periodically forced density dependent fecundity element, and  $p > 1$ . Our density dependent assumption is motivated by the fact that in most fishery models, density effects occur within the first year of life [34,46]. Henson used perturbation along contour methods to study the effects of periodic environments on two age class Leslie-type fisheries models that are subject to 2-periodic forcing [22,34].

We use a mathematical theorem to show that a population governed by an  $n$ -age class Leslie model can be adversely affected by a  $p$ -periodic environment (attenuant cycles). This result is a generalization of that of Cushing and Henson [8], Kon [29,30], Kocic [27], Elaydi and Sacker [11–14] to include population models with age structure. Furthermore, we illustrate that a periodic environment is not always deleterious for such populations. In our age-structured model, a periodic environment does not increase the average total biomass (no resonance).

Section 2 reviews periodically forced single species closed population models without age-structure. The periodic Beverton–Holt and Ricker models are examples of the general model. In Section 3, we introduce the main model, a periodically forced Leslie model with density dependent fecundity element. Such periodically forced discrete dynamical systems generate cyclic or chaotic oscillations. We introduce, in Section 3, a precise mathematical definition of *attenuant* cycles. The average densities of attenuant cycles are less than the average of the carrying capacity in a constant environment. Framework for the support of nonattenuant and attenuant cycles is discussed in Sections 4 and 5, respectively. Section 6 is on the structure of attractors in periodic environments, and the implications of our results are discussed in Section 7.

## 2. Periodic single species population models without age structure

Nonautonomous single species ecological models (without age structure) of the general form

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

have been used to study the long-term dynamics of discretely reproducing populations in periodically varying environments, where  $x(t)$  is the population size at generation  $t$  [17, 18,32,35,36,42,47,49]. The  $C^1$  map  $g : \mathbb{Z}_+ \times [0, \infty) \rightarrow (0, \infty)$  is the per capita growth rate where there exists a *smallest positive integer*  $p$  satisfying  $g(t + p, x) = g(t, x)$ . That is,  $g$  is periodic with period  $p$ .

To understand the long-term dynamics of Model (1), we introduce the following sequence of autonomous models:

$$\begin{aligned} G_0(x) &= xg(0, x), \\ G_1(x) &= xg(1, x), \\ &\vdots \\ G_{p-1}(x) &= xg(p - 1, x). \end{aligned}$$

Notice that

$$G_0(x(0)) = x(1), G_1(x(1)) = x(2), \dots, G_{p-1}(x(p - 1)) = x(p),$$

whenever the set of sequence of population densities  $\{x(0), x(1), \dots\}$  are generated by Model (1). Each  $G_i$  is an autonomous model that describes the population dynamics of a single species in a constant environment. The set of iterates of the  $p$ -periodic dynamical system,  $\{G_0, G_1, \dots, G_{p-1}\}$ , is equivalent to the set of density sequences generated by Model (1). In many ecological models, the  $G_i$  have globally attracting fixed points called the *carrying capacities*. An interesting problem is to find a relationship between the long term dynamics of the  $p$ -periodic dynamical system, Model (1), and the average of the carrying capacities of the  $G_i$ .

**Definition 1.** A periodic orbit of Model (1) is *attenuant (resonant)* if its average value is less (greater) than the average of the carrying capacities of the  $G_i$ .

The nonautonomous Beverton–Holt model,

$$x(t + 1) = \frac{\mu K_t x(t)}{K_t + (\mu - 1)x(t)}, \tag{2}$$

and the nonautonomous Ricker model,

$$x(t + 1) = x(t)e^{r(1-x(t)/K_t)}, \tag{3}$$

are examples of Model (1), where  $K_{t+p} = K_t$ . The coefficients  $r > 0$  and  $\mu > 1$  are the inherent growth rates of the species, and the positive periodic carrying capacity  $K_t$  is a characteristic of the fluctuating habitat or environment.

In the classical (autonomous) Beverton–Holt and Ricker models  $K_t$  is a constant (that is,  $K_t \equiv K$ ). The equilibrium population sizes of both models are 0 and  $K$ . In the Beverton–Holt model every positive initial population size converges to the unique positive equilibrium point  $x_\infty = K$  (carrying capacity) [8,19,20]. The Ricker model has similar long term equilibrium dynamics whenever  $r < 2$ . If  $r > 2$ , the positive equilibrium point becomes unstable and the Ricker model has either cyclic or chaotic long term dynamics [37–40,44].

Periodically forced population models have been used to study the impact of temporal environmental fluctuations on populations. Are populations adversely affected by a periodic environment (relative to a constant environment of the same average carrying capacity)? Coleman [4], Coleman and Frauenthal [5], May [39], Nisbet and Gurney [41] used logistic differential equation models to show that periodic carrying capacities are deleterious. Cushing [8] and Rosenblat [43] have since shown that this result is model dependent. In more recent papers Cushing and Henson [8], Elaydi and Sacker [11–14], Kocic [27] and Kon [28,29] used difference equation models without age structure to show that periodic carrying capacities are deleterious.

### 3. Age structured, periodic population models

To study the effects of age structure and periodic fluctuations on species survival and persistence, we introduce the periodically forced Leslie matrix population model with density dependent fecundity functions. The model is of the form

$$\begin{aligned}
 x_1(t + 1) &= \sum_{i=1}^s x_i(t)g_i(t, x_i(t)), \\
 x_2(t + 1) &= \lambda_1 x_1(t), \\
 &\vdots \\
 x_s(t + 1) &= \lambda_{s-1} x_{s-1}(t),
 \end{aligned} \tag{4}$$

where for each  $i \in \{1, 2, \dots, s\}$ ,  $x_i(t)$  is the population size of the  $i$ th age class at time  $t$  and  $\lambda_i \in (0, 1)$  is the  $i$ th age class constant survival probability per generation. The  $C^1$  map  $g_i : \mathbb{Z}_+ \times [0, \infty) \rightarrow [0, \infty)$  is the fecundity of the  $i$ th age class and there exists a smallest positive integer  $p$  satisfying

$$g_i(t + p, x_i) = g_i(t, x_i)$$

for each  $i$ . We assume that the environment is periodic ( $p > 1$ ). In this model all age classes may reproduce. An age class,  $i$ , is *fertile* if  $g_i(t, x_i) > 0$  at some point  $(t, x_i) \in \mathbb{Z}_+ \times [0, \infty)$ . We assume that a fertile age class remains fertile at all points, that is  $g_i : \mathbb{Z}_+ \times [0, \infty) \rightarrow (0, \infty)$ .

A rescaling of the age classes can be performed to effectively replace the  $\lambda_i$  with 1 giving the  $p$ -periodic Leslie model

$$x_1(t + 1) = \sum_{i=1}^s x_i(t)g_i(t, x_i(t)),$$

$$\begin{aligned}
 x_2(t + 1) &= x_1(t), \\
 &\vdots \\
 x_s(t + 1) &= x_{s-1}(t).
 \end{aligned}
 \tag{5}$$

The Levin–Goodyear age-structured fisheries model [34], studied by Henson [22], is an example of Model (5) with  $p = 2$  and  $s = 2$ .

When only the age class with the largest fertility (class  $L$ ) actually reproduces, Model (5) takes on the following form:

$$\begin{aligned}
 x_1(t + 1) &= x_L(t)g(t, x_L(t)), \\
 x_2(t + 1) &= x_1(t), \\
 &\vdots \\
 x_s(t + 1) &= x_{s-1}(t).
 \end{aligned}
 \tag{6}$$

That is  $g_i = 0$  for  $i \neq L$  in Model (5) and  $g = g_L$ . Since the dynamics of Model (6) are determined by the first  $L$  age classes, we assume  $L = s$  throughout this paper.

To prevent population explosion, we assume that  $\lim_{x \rightarrow \infty} xg(t, x)$  exists. In Model (6) the contribution to the first age class of generation  $t + 1$  by the  $s$ th age class is  $f(t, x_s(t)) = x_s(t)g(t, x_s(t))$ . Note that  $f(t + p, \cdot) = f(t, \cdot)$ . Whenever  $g_s(t, 0) > 1$  for all  $t$ , we say that the contribution to the next generation from the oldest age class is a *pioneer* function [16–18]. When  $f(t, x_i(t)) = \frac{\mu K_i x_i(t)}{K_i + (\mu - 1)x_i(t)}$  (Beverton–Holt), then  $f$  is a bounded pioneer function.

When the environment is constant, Model (6) reduces to

$$\begin{aligned}
 x_1(t + 1) &= x_s(t)g(x_s(t)), \\
 x_2(t + 1) &= x_1(t), \\
 &\vdots \\
 x_s(t + 1) &= x_{s-1}(t).
 \end{aligned}
 \tag{7}$$

In Model (7) the contribution to the first age class of generation  $t + 1$  by the  $s$ th age class is  $f(x_s(t)) = x_s(t)g(x_s(t))$ .

An equilibrium of Model (7) has all age class population sizes the same. This common value of a globally attracting equilibrium vector of the age structured nonperiodic model is called the *carrying capacity*. Model (7) is a discrete time autonomous dynamical system from  $\mathbb{R}_+^s$  to  $\mathbb{R}_+^s$ , which we denote by  $F$ .

For each  $J \in \{0, 1, \dots, p - 1\}$  define  $FJ : \mathbb{R}_+^s \rightarrow \mathbb{R}_+^s$  by

$$FJ(x_1, x_2, \dots, x_s) = (x_s(t)g_s(J, x_s(t)), x_1, x_2, \dots, x_{s-1}).$$

The nonautonomous  $p$ -periodic age-structured model with density dependent fecundity element, Model (6), can be viewed as the compositions of these  $p$  autonomous dynamical systems. One interesting problem is to find a relationship between the carrying capacities, globally attracting fixed points, of the  $FJ$  and the long term dynamics of the  $p$ -periodic Model (6). Note that a cycle for the  $p$ -periodic age-structured model produces cycles in

each age class. The values that each age class goes through are the same but shifted in time. Thus, for each age class the averages of the age class populations over a cycle are the same.

**Definition 2.** A  $k$ -cycle of Model (6) is attenuant (resonant) when each average of the age class populations over the  $k$ -cycle is less (greater) than the average of the carrying capacities of the  $FJ$ .

This generalizes the Cushing–Henson definition of attenuant cycles to include population models with age structure [8].

In this paper, we use Model (6) to derive conditions under which there exists a globally attracting cycle, and we compare the average age-class densities of the cycle (periodic environment) with the average of the carrying capacities (constant environment). That is, we use a simple Leslie model with density dependent periodic fecundity function to show that a periodic environment does not produce resonant cycles.

When  $p = 1$ , the environment is constant and  $F = F0$ . The discrete dynamical system,  $F$ , has several invariant subsets. We use the following notation to describe some of them. Let

$$A = \{x \in \mathbb{R}_+^s : \text{at least one component of } x \text{ is an equilibrium of } f(x) = xg(x)\},$$

$$B_i = \{x \in \mathbb{R}_+^s : x_j = x_i \text{ when } j \geq i \text{ and } x_j = f(x_i) \text{ when } j < i\},$$

and

$$B = \bigcup_{i=1}^s B_i.$$

**Lemma 3.** *A and B are F invariant sets.*

**Proof.** Let  $x \in A = \{x \in \mathbb{R}_+^s : \text{at least one component of } x \text{ is an equilibrium of } f(x) = xg(x)\}$  and the  $i$ th component,  $x_i$ , be an equilibrium of  $f$ . If  $i < s$ , then  $F_{i+1}(x) = x_i$ . So  $F(x) \in A$ . If  $i = s$ , then  $F_1(x) = f(x_s) = x_s$ . Hence, in all cases,  $F(x) \in A$  and  $A$  is invariant under  $F$ .

Let  $x \in B$ . Then there is an  $i \in \{1, 2, \dots, s\}$  such that  $x \in B_i$ . If  $i < s$ , then  $F(x) \in B_{i+1}$ . However, if  $i = s$ , then  $F(x)$  has all coordinates equal to  $f(x_s)$  and  $F(x) \in B_1$ . Thus  $B$  is invariant under  $F$ .  $\square$

#### 4. Nonattenuant and nonresonant cycles

A periodic environment is not always deleterious for a population. That is, it is possible to have the average of the age class populations over an attracting cycle (in a periodic environment) equal to the average of the carrying capacities (in corresponding constant environments). In this section, we show that if the number of age classes,  $s$ , is a multiple of the period of the environment,  $p$ , then the average of the resulting population oscillation in Model (6) is equal to the average of the carrying capacities (nonattenuant and nonresonant

cycle). We also prove that the stable age class distribution in Model (6) is a cycle that has a period which divides  $p$ , whenever each  $G_i$  has a globally attracting equilibrium population size and the number of age classes is a multiple of the period of the environment.

**Theorem 4.** *If for each  $i \in \{0, 1, \dots, p - 1\}$ ,  $G_i$  has an attracting fixed point with basin of attraction  $B_i$  and  $s$  is a multiple of  $p$ , then Model (6) has an attracting  $k$ -cycle with basin of attraction containing  $B_{(s-1) \bmod p} \times B_{(s-2) \bmod p} \times \dots \times B_0$  where  $k$  divides  $p$ .*

**Proof.** For each  $i \in \{0, 1, \dots, p - 1\}$  let  $\bar{x}_i$  be the attracting fixed point for  $G_i$  with basin of attraction  $B_i$ . Since  $s = mp$  for some positive integer  $m$ , we can take the initial age class sizes to be

$$\begin{aligned} &(x_1(0), x_2(0), \dots, x_s(0)) \\ &= (\bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0). \end{aligned}$$

This is  $(\bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0)$  repeated  $m$  times. In one time step the population sizes become

$$\begin{aligned} (x_1(1), x_2(1), \dots, x_s(1)) &= (x_s(0)g(0, x_s(0)), x_1(0), x_2(0), \dots, x_{p-1}(0)) \\ &= (\bar{x}_0g(0, \bar{x}_0), \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_1). \end{aligned}$$

But since  $\bar{x}_0$  is a fixed point of  $G_0$ , we have  $\bar{x}_0g(0, \bar{x}_0) = \bar{x}_0$  and

$$\begin{aligned} &(x_1(1), x_2(1), \dots, x_s(1)) \\ &= (\bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_1). \end{aligned}$$

After another time step the age class sizes are

$$\begin{aligned} &(x_1(2), x_2(2), \dots, x_s(2)) \\ &= (\bar{x}_1g(1, \bar{x}_1), \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \\ &\quad \bar{x}_{p-2}, \dots, \bar{x}_2) \\ &= (\bar{x}_1, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_2), \end{aligned}$$

since  $\bar{x}_1g(1, \bar{x}_1) = G_1(\bar{x}_1) = \bar{x}_1$ . After  $p$  times steps the age classes sizes have returned to

$$(\bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0).$$

Thus,

$$(\bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0)$$

is a choice of initial age class sizes that gets repeated after  $p$  time steps. Since Model (6) is periodic of period  $p$ , this choice of initial age class sizes will continue to repeat every  $p$  time steps. Hence,

$$(\bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0)$$

is a choice of initial age class sizes that gives a periodic orbit. The period of this orbit will usually be  $p$ . But it is possible that it would repeat before  $p$  iterations. If it produces a cycle of period  $k$  and  $k < p$ , then  $k$  must divide  $p$ .

To see that the periodic orbit starting at

$$(\bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0, \dots, \bar{x}_{p-1}, \bar{x}_{p-2}, \dots, \bar{x}_0)$$

is attracting, note that the 2nd iteration of Model (6) is

$$\begin{aligned} x_1(t + 2) &= x_{s-1}(t)g(t + 1, x_{s-1}(t)), \\ x_2(t + 2) &= x_s(t)g(t, x_s(t)), \\ x_3(t + 2) &= x_1(t), \\ &\vdots \\ x_s(t + 2) &= x_{s-2}(t), \end{aligned}$$

and the *s*th iteration is

$$\begin{aligned} x_1(t + s) &= x_1(t)g(t + s - 1, x_1(t)), \\ x_2(t + s) &= x_2(t)g(t + s - 2, x_2(t)), \\ &\vdots \\ x_{s-1}(t + s) &= x_{s-1}(t)g(t + 1, x_{s-1}(t)), \\ x_s(t + s) &= x_s(t)g(t, x_s(t)). \end{aligned}$$

Now fixing  $t = 0$ , we get

$$\begin{aligned} x_1(s) &= x_1(0)g(s - 1, x_1(0)), \\ x_2(s) &= x_2(0)g(s - 2, x_2(0)), \\ &\vdots \\ x_{s-1}(s) &= x_{s-1}(0)g(1, x_{s-1}(0)), \\ x_s(s) &= x_s(0)g(0, x_s(0)). \end{aligned}$$

Since  $s = mp$  and  $g(t + p, x) = g(t, x)$ , the *s*th iteration of each age class *i* is given by the autonomous dynamical system  $G_{(s-i) \bmod p}$ . That is,  $x_i(ns + s) = G_{(s-i) \bmod p}(x_i(ns))$  for  $n \in \mathbb{Z}_+$ . Since  $\bar{x}_{(s-i) \bmod p}$  is an attracting fixed point of  $G_{(s-i) \bmod p}$  with basin  $B_{(s-i) \bmod p}$ ,  $\lim_{n \rightarrow \infty} x_i(ns) = \bar{x}_{(s-i) \bmod p}$  whenever  $x_i(0) \in B_{(s-i) \bmod p}$  and

$$\lim_{n \rightarrow \infty} (x_1(ns), x_2(ns), \dots, x_s(ns)) = (\bar{x}_{(s-1) \bmod p}, \bar{x}_{(s-2) \bmod p}, \dots, \bar{x}_0).$$

The continuity of Model (6) together with the periodicity of the orbit of

$$(\bar{x}_{(s-1) \bmod p}, \bar{x}_{(s-2) \bmod p}, \dots, \bar{x}_0),$$

prove that the orbit of

$$(\bar{x}_{(s-1) \bmod p}, \bar{x}_{(s-2) \bmod p}, \dots, \bar{x}_0)$$

is an attracting cycle of period *k* with basin of attraction containing

$$B_{(s-1) \bmod p} \times B_{(s-2) \bmod p} \times \dots \times B_0,$$

where *k* divides *p*. □



The following corollary follows from Theorem 4 when each  $B_i = (0, \infty)$ .

**Corollary 5.** *If for each  $i \in \{0, 1, \dots, p - 1\}$ ,  $G_i$  has a globally attracting fixed point on  $(0, \infty)$  and  $s$  is a multiple of  $p$ , then Model (6) has a globally attracting  $k$ -cycle on  $(0, \infty) \times (0, \infty) \times \dots \times (0, \infty)$  where  $k$  divides  $p$ .*

**Corollary 6.** *If  $\bar{x}$  is a globally attracting fixed point for  $G(x) = xg(x)$  on  $(0, \infty)$ , then  $(\bar{x}, \bar{x}, \dots, \bar{x})$  is a globally attracting fixed equilibrium point of Model (7) on  $(0, \infty) \times (0, \infty) \times \dots \times (0, \infty)$ .*

The proof follows by noting that the proof of Theorem 4 did not make use of the fact that  $p$  was the smallest positive integer satisfying  $g(t + p, x) = g(t, x)$ .

**Corollary 7.** *If for each  $i \in \{0, 1, \dots, p - 1\}$ ,  $G_i$  has a globally attracting fixed point on  $(0, \infty)$  and  $s$  is a multiple of  $p$ , then the global attracting  $k$ -cycle of Model (6) on  $(0, \infty) \times (0, \infty) \times \dots \times (0, \infty)$  is nonattenuant and nonresonant.*

**Proof.** From the proof of Theorem 4, each point in the attracting  $k$ -cycle consists of a permutation of the globally attracting fixed points of the  $G_j$  repeated  $m$  times. Each point on the  $k$ -cycle is a cyclic permutation of the others, and the average of this  $k$ -cycle is a vector with all coordinates equal to the average of the globally attracting fixed points of the  $G_j$ , which is also the average of carrying capacities of the  $G_j$ . Hence, this globally attracting  $k$ -cycle fails to be either attenuant or resonant.  $\square$

To demonstrate Theorem 4 and Corollary 7 in the Beverton–Holt and Ricker models with age-structure we consider the following example.

**Example 8.** When the fertility function

$$g(t, x) = \frac{\mu K_t}{K_t + (\mu - 1)x}$$

and  $K_t$  is periodic with period  $p$ , the Beverton–Holt maps  $G_j$  have carrying capacity  $K_j$  and the  $K_j$  are also their global attracting fixed points. However, if the fertility function

$$g(t, x) = e^{r(1-x/K_t)}$$

with  $0 < r < 2$  and  $K_t$  is periodic with period  $p$ , the Ricker maps  $G_j$  have carrying capacity  $K_j$  and the  $K_j$  are also their global attracting fixed points. In either case, if the number of age classes equals the period of  $K_t$ , then the orbit of

$$(K_{s-1}, K_{s-2}, \dots, K_0)$$

is a globally attracting, nonattenuant, nonresonant  $k$ -cycle where  $k$  divides  $p$ .

### 5. Attenuant cycles

A periodic environment is disadvantageous for a population whenever there is no synchrony between the number of age classes and the period of the environment. To illustrate this, we give conditions for our age structured Model (6) to have a globally stable attenuant cycle. Others have used either continuous-time (logistic differential equation) or discrete-time (Beverton–Holt) single species population models *without* age-structure to show that it is possible for a periodic environment to be disadvantageous for a population [8,11–14, 22,26,28,29].

Model (2) with nonconstant carrying capacities has a globally attracting positive attenuant cycle. To generalize this result to include age structured models, we make the following assumption in Model (6):

(A): Every  $L$ -periodic dynamical system formed from a subset of

$$\{G_0, G_1, \dots, G_{p-1}\}$$

and consisting of at least two of the  $G_j$  has a globally attracting positive attenuant cycle.

In Model (2),

$$G_j(x) = \frac{\mu K_j x}{K_j + (\mu - 1)x}.$$

Picking a subset of the  $\{G_0, G_1, \dots, G_{p-1}\}$  is equivalent to picking the corresponding subset of  $\{K_0, K_1, \dots, K_{p-1}\}$ . This subset generates a new Model (2) and hence must have a globally attracting positive attenuant cycle. Thus, every  $L$ -periodic subset of  $\{G_0, G_1, \dots, G_{p-1}\}$  consisting of at least two of the  $G_j$  has a globally attracting positive attenuant cycle (assumption (A)).

**Theorem 9.** *If Model (6) satisfies assumption (A) and  $s$  is not a multiple of  $p$ , then the model has a globally attracting positive attenuant cycle.*

**Proof.** Let

$$(x_1(0), x_2(0), \dots, x_s(0)) = (x_1, x_2, \dots, x_s)$$

be a fixed set of initial age class population densities. Let  $G_k = G_{k \bmod p}$ . The fixed initial condition is mapped to  $(G_0(x_s), x_1, x_2, \dots, x_{s-1})$  by Model (6). The next image is

$$(G_1(x_{s-1}), G_0(x_s), x_1, x_2, \dots, x_{s-2}).$$

After  $s$  iterations the image is

$$(G_{s-1}(x_1), G_{s-2}(x_2), \dots, G_1(x_{s-1}), G_0(x_s)).$$

The image after  $s + 1$  iterations is

$$(G_s(G_0(x_s)), G_{s-1}(x_1), G_{s-2}(x_2), \dots, G_1(x_{s-1})).$$

After  $2s$  iterations the image is

$$(G_{2s-1}(G_{s-1}(x_1)), G_{2s-2}(G_{s-2}(x_2)), \dots, G_{s+1}(G_1(x_{s-1})), G_s(G_0(x_s))).$$

After  $3s$  iterations the image is

$$(G_{3s-1}(G_{2s-1}(G_{s-1}(x_1))), G_{3s-2}(G_{2s-2}(G_{s-2}(x_2))), \dots, G_{2s+1}(G_{s+1}(G_1(x_{s-1}))), G_{2s}(G_s(G_0(x_s))).$$

After  $ps$  iterations the image is

$$(G_{ps-1}(\dots(G_{3s-1}(G_{2s-1}(G_{s-1}(x_1))))\dots), G_{ps-2}(\dots(G_{3s-2}(G_{2s-2}(G_{s-2}(x_2))))\dots), \dots, G_{ps-s+1}(\dots(G_{2s+1}(G_{s+1}(G_1(x_{s-1}))))\dots), G_{ps-s}(\dots(G_{2s}(G_s(G_0(x_s))))\dots)).$$

Observe that the  $i$ th image of  $x_j$  under the composition map

$$G_{ps-j} \circ \dots \circ G_{3s-j} \circ G_{2s-j} \circ G_{s-j}$$

is the population density of the  $j$ th age class after  $ips$  generations. Since  $s$  is not a multiple of  $p$ , the composition

$$G_{ps-j} \circ \dots \circ G_{3s-j} \circ G_{2s-j} \circ G_{s-j}$$

is made up of at least two different  $G_k$ . Therefore, by assumption (A), the periodic dynamical system generated by

$$\{G_{s-j}, G_{2s-j}, G_{3s-j}, \dots, G_{ps-j}\}$$

has a globally attracting positive attenuant cycle. We denote the first point on this  $r$ -cycle by  $y_j$ . By a theorem of Elaydi and Sacker [11–15], there is a positive integer  $m$  such that  $mr = p$ .

Next, we show that  $(y_1, y_2, \dots, y_s)$  is the first point on a globally attracting positive attenuant cycle for Model (6). Since each  $y_j$  is the first point on a globally attracting cycle whose period divides  $p$ , after  $ps$  iterations Model (6) maps  $(y_1, y_2, \dots, y_s)$  to itself. That is,  $(y_1, y_2, \dots, y_s)$  is the initial point on a cycle for Model (6).

Now, we show that the cycle is globally attracting. Using  $ps$  iterations of Model (6) and the global attracting nature of each  $y_j$ , we see that any initial condition limits on  $(y_1, y_2, \dots, y_s)$ . The continuity of Model (6) implies that the cycle starting at  $(y_1, y_2, \dots, y_s)$  is globally attracting. To see that this orbit is attenuant, we consider the orbit of the first age class. We break the first  $ps$  iterates of the orbit into groups that are  $s$  iterations apart. These groups consist of the first  $p$  iterations of  $y_j$  under the periodic dynamical system  $\{G_{s-j}, G_{2s-j}, G_{3s-j}, \dots, G_{ps-j}\}$ . Since the cycle starting at  $y_j$  using the periodic dynamical system  $\{G_{s-j}, G_{2s-j}, G_{3s-j}, \dots, G_{ps-j}\}$  is attenuant, the average of the corresponding group is less than the average of the carrying capacities of  $\{G_{s-j}, G_{2s-j}, G_{3s-j}, \dots, G_{ps-j}\}$ . Since the average of the averages is less than the average of larger averages, the average of the first  $ps$  iterates of  $y_1$  is less than the average of the carrying capacities of  $\{G_0, G_1, G_2, \dots, G_{ps-1}\}$ . Each of the  $G_k$  appear in this list the

same number of times, the average of the carrying capacities of  $\{G_0, G_1, G_2, \dots, G_{ps-1}\}$  equals the average of the carrying capacities of  $\{G_0, G_1, G_2, \dots, G_{p-1}\}$ . So the first age class satisfies the inequality of an attenuant cycle. Each of the other age classes have orbits which are time shifts of that for the first age class. Thus each age class satisfies the inequality of an attenuant cycle and hence the globally attracting positive cycle is attenuant.  $\square$

To apply Theorem 9, we consider Model (6) with 2 age classes in a period 3 environment. Since every periodic dynamical system formed from a subset of  $\{G_0, G_1, G_2\}$  has a globally attracting positive attenuant cycle, let  $y_1$  be the first point on this cycle for the periodic dynamical system  $\{G_1, G_0, G_2\}$ . Let  $G_1(y_1) = y_2$  and  $G_0(y_2) = y_3$ . Now  $G_2(y_3) = y_1$  since  $y_1$  has period 3 for this periodic dynamical system. The initial population sizes  $(y_1, y_2)$  are mapped to  $(G_0(y_2), y_1) = (y_3, y_1)$ . The next image is  $(G_1(y_1), y_3) = (y_2, y_3)$ . The third image is  $(G_2(y_3), y_2) = (y_1, y_2)$ . Thus  $(y_1, y_2)$  has period 3 a divisor of  $ps = 6$  for Model (6). Note that both age classes cycle through permutations of the attenuant cycle  $\{y_1, y_2, y_3\}$  and hence  $(y_1, y_2)$  starts an attenuant cycle for the model. Next, we demonstrate this with a Beverton–Holt example.

**Example 10.** In Model (6) let the fertility function

$$g(t, x) = \frac{\mu K_t}{K_t + (\mu - 1)x},$$

where  $K_t = K_{t+3}$  and the number of age classes  $s = 2$ . Then the corresponding carrying capacities of the Beverton–Holt models  $G_0, G_1$  and  $G_2$  are  $K_0, K_1$  and  $K_2$ , respectively. The fixed point of  $G_2 \circ G_0 \circ G_1$  is

$$y_1 = \frac{(\mu^2 + \mu + 1)K_0K_1K_2}{K_0K_2 + \mu K_1K_2 + \mu^2 K_0K_1}.$$

Now

$$y_2 = G_1(y_1) = \frac{(\mu^2 + \mu + 1)K_0K_1K_2}{K_1K_2 + \mu K_0K_1 + \mu^2 K_0K_2}$$

and

$$y_3 = G_0(y_2) = G_0(G_1(y_1)) = \frac{(\mu^2 + \mu + 1)K_0K_1K_2}{K_0K_1 + \mu K_0K_2 + \mu^2 K_1K_2}.$$

The initial condition  $(y_1, y_2)$  is the starting point for a globally attracting positive attenuant 3-cycle (Theorem 9).

### 6. Multiple overlapping chaotic attractors

In constant environments, single species discrete-time population models without age structure and without the allee effect, like the Beverton–Holt and Ricker models, do not have multiple (coexisting) attractors [19,20,33]. However, in periodic environments the Ricker model without age structure and without the allee effect admit multiple cyclic (non-interval) or chaotic (interval) attractors [16–18]. In this section, we discuss the implications

of these attractors on periodic age structured models. Periodicity is not the only mechanism for generating multiple attractors. In constant environments, single species discrete-time population models with age structure and without the allee effect can have multiple (coexisting) attractors [47].

An open set  $U$  is a *trapping region* for a continuous dynamical system  $F : X \rightarrow X$  if  $F(\overline{U}) \subset U$  where  $X$  is a locally compact metric space and  $\overline{U}$  is a compact subset of  $X$ . A trapping region for  $F, U$ , generates the nonempty compact attractor  $\Lambda = \bigcap_{i=0}^{\infty} F^i(\overline{U})$ .

**Lemma 11.** *Let  $F$  and  $G$  be continuous dynamical systems on  $X$ . If  $U$  is a trapping region for both  $F$  and  $G$ , then  $U$  is a trapping region for both  $G \circ F$  and  $F \circ G$ .*

**Proof.** Since  $F(\overline{U}) \subset U$  and  $G(\overline{U}) \subset U$ ,  $G \circ F(\overline{U}) \subset U$  and  $F \circ G(\overline{U}) \subset U$ . Thus  $U$  is a trapping region for both  $G \circ F$  and  $F \circ G$ .  $\square$

By Lemma 11, when any two dynamical systems have the same trapping region,  $U$ , then the systems and their compositions have attractors in  $U$ .

We will use the following perturbation result of Franke and Selgrade [16].

**Lemma 12.** *Let  $F$  be a continuous dynamical system on  $X$ . If  $U$  is a trapping region for  $F$ , then there is a neighborhood  $V$  of  $F$  in the function space of continuous maps on  $X$  such that  $G \in V$  implies that  $U$  is a trapping region for  $G$ .*

Now we make a connection between trapping regions for the one-dimensional model,  $f(x_s) = x_s g(x_s)$ , and trapping regions for the autonomous  $s$ -dimensional age class model, System (7).

**Theorem 13.** *If  $U \subset \mathbb{R}_+$  is a trapping region for  $f(x_s) = x_s g(x_s)$  with attractor  $\Lambda$ , then the positively  $F$ -invariant set,  $U \times U \times \dots \times U \subset \mathbb{R}_+^s$ , is a trapping region for  $F^s$  with attractor  $\Lambda \times \Lambda \times \dots \times \Lambda \subset \mathbb{R}_+^s$ , where  $F : \mathbb{R}_+^s \rightarrow \mathbb{R}_+^s$  is System (7). Furthermore,  $\Lambda \times \Lambda \times \dots \times \Lambda$  is an attractor for  $F$ .*

**Proof.** Since  $U$  is a trapping region for  $f$ ,  $f(\overline{U}) \subset U$ .

$$F_1(\overline{U \times U \times \dots \times U}) = f(\overline{U}) \subset U.$$

For  $i \in \{2, 3, \dots, s\}$ ,  $F_i(U \times U \times \dots \times U) = U$ . Thus  $U \times U \times \dots \times U$  is  $F$  invariant. For each  $i \in \{1, 2, \dots, s\}$ ,

$$F_i^s(\overline{U \times U \times \dots \times U}) = f(\overline{U}) \subset U.$$

Hence,  $U \times U \times \dots \times U$  is a trapping region for  $F^s$ . Now

$$F^s(\overline{U \times U \times \dots \times U}) = f(\overline{U}) \times f(\overline{U}) \times \dots \times f(\overline{U})$$

so

$$\begin{aligned} \bigcap_{i=0}^{\infty} F^{is}(\overline{U \times U \times \dots \times U}) &= \bigcap_{i=0}^{\infty} f^i(\overline{U}) \times f^i(\overline{U}) \times \dots \times f^i(\overline{U}) \\ &= \Lambda \times \Lambda \times \dots \times \Lambda. \end{aligned}$$

Since  $f(\bar{U})$  is a compact subset of the open set  $U$  and disjoint from the complement of  $U$  in  $\mathbb{R}_+$ ,  $\alpha = \inf\{|p - q|: p \in f(\bar{U}) \text{ and } q \in \mathbb{R}_+ \setminus U\} > 0$ . For each  $i \in \{1, 2, \dots, s\}$  let  $U_i = \{q \in \mathbb{R}_+: |p - q| < \alpha/i \text{ for some } p \in f(\bar{U})\}$ . Then each  $U_i$  is open and

$$f(\bar{U}) \subset U_s \subset \bar{U}_s \subset U_{s-1} \subset \bar{U}_{s-1} \subset U_{s-2} \subset \dots \subset \bar{U}_2 \subset U_1 \subset U.$$

Thus,  $f(\bar{U}_1) \subset f(\bar{U}) \subset U_1$  and each  $\bar{U}_i$  is a compact subset of  $\bar{U}$ .

$$\begin{aligned} &F(\overline{U_s \times U_{s-1} \times \dots \times U_1}) \\ &= f(\bar{U}_1) \times \bar{U}_s \times \bar{U}_{s-1} \times \dots \times \bar{U}_2 \subset U_s \times U_{s-1} \times \dots \times U_1. \end{aligned}$$

Hence  $U_s \times U_{s-1} \times \dots \times U_1$  is a trapping region for  $F$  with attractor  $\Lambda \times \Lambda \times \dots \times \Lambda$ .  $\square$

To demonstrate Theorem 13 with a specific model, we consider System (7) with two age classes and classic Ricker growth function.

**Example 14.** In System (7) let  $s = 2$  and  $g(x) = e^{r(1-x/K)}$  where  $r$  and  $K$  are positive.

When  $r = 2.1$  and  $K = 1$ ,  $f(x) = xe^{r(1-x/K)}$  has a 2-cycle attractor,  $\Lambda$ , with trapping region,  $U$ , consisting of two open intervals.  $\Lambda \times \Lambda$  is a 4 point attractor for Example 14 with trapping region consisting of four rectangles. As shown in [47],  $\Lambda \times \Lambda$  is a 4-cycle periodic attractor.

When  $r = 2.8$  and  $K = 1$ ,  $f(x) = xe^{r(1-x/K)}$  has a chaotic attractor with positive Lyapunov exponent,  $\Lambda$ , consisting of two closed intervals. Its trapping region,  $U$ , consists of two open intervals.  $\Lambda \times \Lambda$ , a chaotic attractor with positive Lyapunov exponents for Example 14, consists of four closed rectangles. The trapping region consists of four open rectangles. The four rectangles in  $\Lambda \times \Lambda$  “effectively rotate”  $90^\circ$  under  $F$  so that the diagonal pairs are invariant under  $F^2$ . Hence  $F^2$  has two coexisting chaotic attractors.

Figure 1 shows the four chaotic rectangles. This figure also shows that each of the invariant sets,  $A$  and  $B$ , given in Lemma 3 contain four piece chaotic subsets (blue lines and black curves). These sets are attractors for  $F$  restricted to  $A$  and  $B$ , respectively. A trapping region for the chaotic attractor in  $A$  is  $\{1\} \times U \cup U \times \{1\}$  and a trapping region for the chaotic attractor in  $B$  is  $\{(x, x) \in \mathbb{R}_+^2: x \in U\} \cup \{(f(x), x) \in \mathbb{R}_+^2: x \in U\}$ .

The next example can be viewed as making Example 14 periodic with period 2.

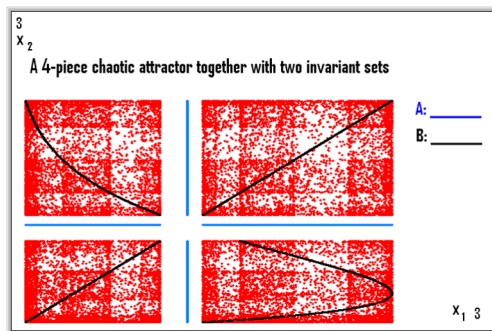


Fig. 1. 4-piece chaotic attractor together with two invariant sets (A, blue, and B, black).

**Example 15.** In System (6) let  $s = 2$  and  $g(t, x) = e^{r(1-x/(K+c(-1)^t))}$  where  $r, c$  and  $K$  are positive.

When  $r = 2.1, K = 1,$  and  $c$  is a small positive number, the periodic Ricker model without age structure,  $f(t, x) = xe^{r(1-x/(K+c(-1)^t))}$ , has two 2-cycle attractors as predicted by the perturbation theorem of Henson [21,22]. Each of these 2-cycle attractors produce a 4-cycle attractor for the corresponding 2-periodic age structured Ricker model, Example 15, as seen in Fig. 2 where  $c = 0.1$ .

Franke and Selgrade studied attractors in periodic dynamical systems [16]. In their framework, an attractor for the 2-periodic dynamical system  $\{F_0, F_1\}$  consists of an attractor for the composition map  $F_1 \circ F_0$  together with the image of this attractor under  $F_0$ . When  $c = 0,$  it is easy to see that  $F_1 = F_0 = F$  and  $F_1 \circ F_0 = F^2$  (Example 15). In addition, when  $r = 2.8$  and  $K = 1,$  the two chaotic attractors of  $F^2$  are pairs of diagonal rectangles that are mapped onto each other under  $F$  iteration. Lemma 12 implies that when  $c$  is small, the trapping regions for  $F^2$  are also trapping regions for  $F_1 \circ F_0$ . Thus,  $F_1 \circ F_0$  has two attractors which are “close” to the attractors of  $F^2$ . The images of these attractors under  $F_0,$  however, do not need to be each other. In this case,  $\{F_0, F_1\}$  has two distinct attractors. Figure 3 shows two overlapping attractors with positive Lyapunov ex-

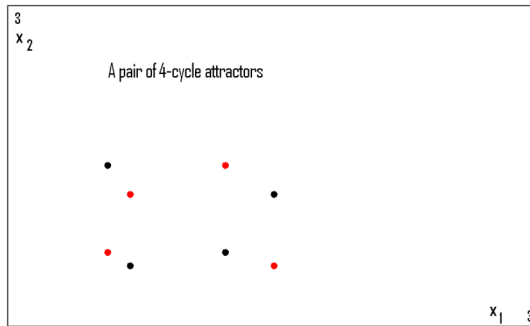


Fig. 2. Two coexisting period 4 attractors.

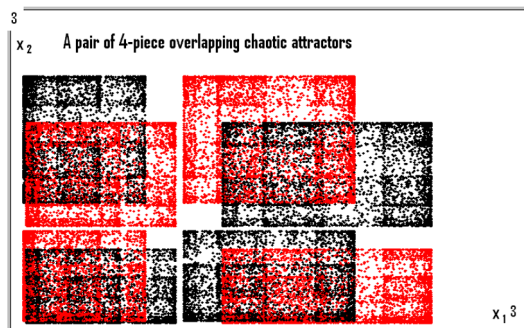


Fig. 3. A 4-piece chaotic attractor (black) coexisting with another 4-piece chaotic attractor (red) and the two attractors overlap.

ponents (black and red) when  $c = 0.1$ . A point starting in one of the black major diagonal rectangles stays in the black rectangles for all time, while a point starting in one of the red minor diagonal rectangles stays in the red rectangles for all time.

## 7. Conclusion

This paper focuses on an old ecological question. Are species adversely affected by a periodic environment relative to a constant environment of the same average carrying capacity? Henson used a “contour method” to study the effect of periodicity in the Levin–Goodyear Leslie-type 2-age class fisheries model with 2-periodic forcing. We use a  $p$ -periodically forced,  $n$ -age class, discrete time population model to study the effects of periodic fluctuations and age-structure on populations ( $p > 1$ ).

Results of Coleman [4], Coleman and Frauenthal [5], Nisbet and Gurney [41], and Rosenblat [43] on the continuous-time logistic equation (without age-structure) implied that a periodic carrying capacity is deleterious. Cushing [8] and Rosenblat [43] have since shown that this assertion is model dependent.

In a recent paper, Cushing showed that a periodic environment is always deleterious for populations modeled by a class of monotone difference equations without age-structure. Our results support this assertion whenever there is no synchrony between the number of age classes and the period of the environment. In addition, in contrast to Cushing’s results for monotone equations and the periodic Beverton–Holt model (without age structure), we show that a periodic environment is not always deleterious for age-structured population models. We also show that a periodic environment does not generate resonant cycles in our age-structured population model.

Periodically forced population models with or without age-structure are capable of generating multiple attractors with complicated structures [2,16,21,23,47–49]. Studies on the structures of the coexisting attractors and their basin boundaries would be welcome [1]. The use of periodicity as a mechanism to increase the number of attractors combined with age-structure may increase the likelihood of species survival in periodically varying environments.

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