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Signature Function for Predicting Resonant and Attenuant Population 2-cycles

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Abstract Populations are either enhanced via resonant cycles or suppressed via attenuant cycles by periodic environments. We develop a signature function for predicting the response of discretely reproducing populations to 2-periodic fluctuations of both a characteristic of the environment (carrying capacity), and a characteristic of the population (inherent growth rate). Our signature function is the sign of a weighted sum of the relative strengths of the oscillations of the carrying capacity and the demographic characteristic. Periodic environments are deleterious for populations when the signature function is negative. However, positive signature functions signal favorable environments. We compute the signature functions of six classical discrete-time single species population models, and use the functions to determine regions in parameter space that are either favorable or detrimental to the populations. The two-parameter classical models include the Ricker, Beverton-Holt, Logistic, and Maynard Smith models.

Keywords Attenuance · Periodic carrying capacity · Periodic demographic characteristic · Signature function · Resonance

1. Introduction

The importance of the carrying capacity and the demographic characteristic of a population (growth rate), both in controlling population growth and predicting population trends in constant or periodic environments, in real-world populations is well-established (Moran, 1950; Nicholson, 1954; Ricker, 1954; Beverton and Holt, 1957; Utida, 1957; Pennycuick et al., 1968; Smith, 1968; Hassell, 1974; May, 1974a,b; Smith, 1974; Hassell et al., 1976; May and Oster, 1976; May, 1977; Coleman, 1978; Fisher et al., 1979; Jillson, 1980; Rosenblat, 1980; Nisbet and

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Gurney, 1982; Nobile et al., 1982; Coleman and Frauenthal, 1983; Rosenkranz, 1983; Kot and Schaffer, 1984; Cull, 1986; Cull, 1988; Rodriguez, 1988; Yodzis, 1989; Li, 1992; Kocic and Ladas, 1993; Elaydi, 1994; Begon et al., 1996; Henson and Cushing, 1997; Costantino et al., 1998; Henson, 1999; Henson et al., 1999; Elaydi, 2000; Henson, 2000; Cushing and Henson, 2001; Selgrade and Roberds, 2001; Elaydi and Yakubu, 2002; Cull, 2003; Elaydi and Sacker, 2003, 2005, in press-a,b; Yakubu, 2005; Kocic, in press; Kon, in press-a,b). In constant environments, many classical, discrete-time single-species, population models have at least the two parameters, carrying capacity and demographic characteristic of the species (Moran, 1950; Nicholson, 1954; Ricker, 1954; Beverton and Holt, 1957; Pennycuick et al., 1968; Smith, 1968; Hassell, 1974; May, 1974a,b; Smith, 1974; Hassell et al., 1976; May and Oster, 1976; May, 1977; Nisbet and Gurney, 1982; Rosenkranz, 1983; Cull, 1986, 1988, 2003; Yodzis, 1989; Begon et al., 1996; Elaydi, 2000; Cushing and Henson, 2001; Franke and Yakubu, 2005a,b,c). What are the responses of these populations to periodic fluctuations in the two or more parameters? Are the populations adversely affected by a periodic environment relative to a constant environment?

The controlled laboratory experiments 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 (Jillson, 1980; Henson and Cushing, 1997; Costantino et al., 1998; Henson, 1999, 2000; Henson et al., 1999; Cushing and Henson, 2001; Franke and Selgrade, 2003). Mathematical analysis and laboratory experiments were used in Henson and Cushing (1997), Costantino et al. (1998), Henson (1999, 2000), Henson et al. (1999) 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 to show that a periodic environment is deleterious (PColeman, 1978; Rosenblat, 1980; Coleman and Frauenthal, 1983; Cushing and Henson, 2001). That is, the average of the resulting oscillations in the periodic environment is less than the average of the carrying capacities in corresponding constant environments. Cushing and Henson obtained similar results for 2-periodic monotone models (Cushing and Henson, 2001). Elaydi and Sacker (2003, 2005, in press-a,b), Franke and Yakubu (2005a,b), Kocic (in press), and Kon (in press-a,b) have since extended these results to include *p-periodic* Beverton–Holt population models with or without age-structure, where $p > 2$. These results are known to be model-dependent (Cushing and Henson, 2001). In almost all the theoretical studies, with only a few exceptions (see Elaydi and Sacker, 2003, 2005, in press-a,b; Franke and Yakubu, 2005a,b,c), *only* the carrying capacity of the species (one parameter) is periodically forced.

Periodic fluctuations, common in nature, usually diminish (enhance) populations via attenuant (resonant) stable cycles. In this paper, we focus on the effects of 2-periodic forcing of *both* carrying capacity and demographic characteristic of species on discretely reproducing populations. Although this is a 2-parameter problem, the bifurcation is asymmetric in the parameters. That is, variation *only* in carrying capacity generates a 2-cycle but variation *only* in demographic characteristics does not; whenever the 2-cycle bifurcates from the carrying capacity (fixed point). It is known that unimodal maps under period-2 forcing in the parameters routinely have up to three coexisting 2-cycles. This was shown for the Logistic map by Kot and Schaffer (1984), and for the Ricker map by Rodriguez (1988).

We show that, the relative strengths of the oscillations of carrying capacity and demographic characteristics are critical factors in determining whether populations are either diminished or enhanced. We develop a signature function, $\mathcal{R}_{\mathrm{d}}$, for determining whether the average total biomass is suppressed via attenuance stable 2-cycles or enhanced via resonance stable 2-cycles. $\mathcal{R}_{\mathrm{d}}$ is the sign of a weighted sum of the relative strengths of the oscillations of carrying capacity and demographic characteristic of species. We demonstrate that, when oscillations are small and the environment is 2-periodic the population diminishes when $\mathcal{R}_{\mathrm{d}}$ is negative, while the population is enhanced when $\mathcal{R}_{\mathrm{d}}$ is positive. Consequently, a change in relative strengths of oscillations of carrying capacity and demographic characteristic of a species is capable of shifting population dynamics from attenuance to resonance cycles and vice versa. Typically, this dramatic shift is not possible in population models with a single fluctuating parameter (Henson, 1999). To illustrate this in specific ecological population models, we compute $\mathcal{R}_{\mathrm{d}}$ for six classical, single-species discrete-time models (Ricker, 1954; Beverton and Holt, 1957; Pennycuick et al., 1968; Smith, 1968; Hassell, 1974; Smith, 1974) (including the Beverton–Holt, Ricker, and Maynard Smith periodic models), and provide parameter regimes for the occurrence of stable attenuant and resonant cycles in the models.

Section 2 introduces a general framework for studying the impact of environmental fluctuations on discrete-time population models with two or more fluctuating parameters. Six classical, single-species discrete-time, population models, including the Beverton–Holt, Ricker and Maynard Smith models, are examples of the general model. Also, in Sect. 2, precise mathematical definitions of attenuant and resonant cycles are stated. In Sect. 3, we prove that small 2-periodic perturbations of carrying capacity and demographic characteristic of populations produce 2-cycle populations. Henson used a small perturbation of only one parameter, the carrying capacity, to obtain a similar result (Henson, 1999). The signature function, $\mathcal{R}_{\mathrm{d}}$, for 2-species Kolmogorov type discrete-time population models with 2-periodic forcing of two parameters is introduced in Sect. 3. $\mathcal{R}_{\mathrm{d}}$ for six classical, single-species, (parametric) population models, and regions in parameter space for the support of attenuant or resonant cycles in the models are given in Sect. 4. In Sects. 3, 4, and 5, we assume that a 2-cycle must, for small forcing, be close to the carrying capacity. However, the carrying capacity does not have to be the only source of 2-cycles.

To compute $\mathcal{R}_{\mathrm{d}}$ for the other coexisting 2-cycles, we assume in Sects. 6, 7, and 8, that as forcing is introduced into the system two 2-cycles bifurcate from a 2-cycle which is present in the unforced system. That is, we assume that two 2-cycles "come off of" (the two different phases of) a 2-cycle in the unforced model. In Sect. 6, we prove that small 2-periodic perturbations of a 2-cycle of the unforced system produce two 2-cycle populations. Signature functions, $\mathcal{R}_{\mathrm{d}}$, for 2-species Kolmogorov-type, discrete-time, population models with 2-periodic forcing of 2-cycles are introduced in Sect. 7. $\mathcal{R}_{\mathrm{d}}$ for the Ricker and Logistic models, and regions in parameter space for the support of attenuant or resonant coexisting 2-cycles in the models are given in Sect. 8. The implications of our results are discussed in Sect. 9, and technical details of the $\mathcal{R}_{\mathrm{d}}$ derivation are given in the Appendix.

2. Classical parametric population models

Most single species ecological models have two or more model parameters. In 1999, Henson studies the effects of 2-periodic forcing of a single model parameter, the carrying capacity, on the average biomass. To study the combined effects of 2-periodic forcing of two model parameters, the carrying capacity and the demographic characteristic of the species, we consider population models of the general form

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

where $x(t)$ is the population size at generation t, r is the demographic characteristic of the species, and k is the carrying capacity, i.e., $g(k, r, k) = 1$. The per capita growth rate $g \in C^3(\mathring{\mathbb{R}}_+ \times \mathring{\mathbb{R}}_+ \times \mathring{\mathbb{R}}_+,)$ where$\mathbb{R}_+ = [0, \infty)$ and $\mathring{\mathbb{R}}_+ = (0, \infty)$.

For each pair of positive constants k and r, define

$$f_{k,r} : \mathbb{R}_+ \to \mathbb{R}_+$$

by

$$f_{k,r}(x) = xg(k, r, x).$$

The set of iterates of $f_{k,r}$ is equivalent to the set of density sequences generated by Model (1).

Table 1 is a list of specific classical examples of (Model 1) from the literature. Model I and Model II in Table 1 are the classic Ricker and Beverton–Holt models, respectively. The carrying capacity, k, is a globally attracting fixed point for the Beverton–Holt model for all $k > 0$ and $r > 1$. However, in Ricker's model for all $k > 0$, the carrying capacity is a globally attracting fixed point when $0 < r < 2$ (see column 3 of Table 1 for stability conditions) and locally repelling when $r > 2$

Table 1 Examples of multiparameter population models.

Model number	Model	Parameters giving stable carrying capacity, $k > 0$	References
I	$f_{k,r}(x) = x\exp(r(1 - \frac{x}{k}))$	$0 < r < 2$	Moran (1950) Ricker (1954) Smith (1974) May (1974a,b) Fisher et al. (1979)
II	$\frac{krx}{k+(r-1)x}$	$1 < r$	Beverton and Holt (1957) May (1974a,b)
III	$x(1 + r - \frac{rx}{k})$, $0 \le x \le \frac{k(1+r)}{r}$	$0 < r < 2$	Logistic model (Elaydi, 2000)
IV	$\frac{(1+k)^r x}{(1+x)^r}$	$0 < r < \frac{2(1+k)}{k}$	Hassell (1974)
V	$\frac{k^2 rx}{k^2+(r-1)x^2}$	$1 < r$	Smith (1974)
VI	$\frac{k^c rx}{k^c+(r-1)x^c}$	$1 < r, c(r-1) < 2r$	Smith (1974)

(Moran, 1950; Nicholson, 1954; Ricker, 1954; May, 1974a,b, 1977; May and Oster, 1976). The maximal growth rates of the populations described by the Beverton–Holt and Ricker models are r and e^r, respectively.

When both the carrying capacity and the demographic characteristics are 2-periodically forced, then Model (1) becomes

$$x(t+1) = x(t)g(k\,(1+\alpha(-1)^t), r(1+\beta(-1)^t), x(t)), \tag{2}$$

where the relative strengths of the perturbations $\alpha, \beta \in (-1, 1)$. Unimodal maps with period-2 forcing routinely have up to three coexisting 2-cycles. For the logistic and Ricker maps, these results were obtained by Kot and Schaffer (1984) and Rodriguez (1988), respectively. In Sect. 4, we study all six 2-periodically forced examples of Table 1.

When

$$x_1 = x_0 g(k(1+\alpha), r(1+\beta), x_0)$$

and

$$x_0 = x_1 g(k(1-\alpha), r(1-\beta), x_1),$$

then $\{x_0, x_1\}$ is a 2-cycle for Model (2). Depending on model parameters, 2-periodic dynamical systems have globally stable 2-cycles (Franke and Yakubu, 2005a,b,c). In the next section, we obtain conditions for the global stability of the 2-cycle of Model (2) under the assumption that the 2-cycle must, for small forcing, be close to the carrying capacity. In general, the carrying capacity does not have to be the only source of 2-cycles. The other two 2-cycles come off of the 2-cycle in the unforced logistic and Ricker maps.

When a 2-cycle comes off of the carrying capacity k, we use the following definition to compare the average of the 2-cycle with the carrying capacity k.

Definition 1. A 2-cycle of Model (2) is attenuant (resonant) if its average value is less (greater) than the carrying capacity k (Cushing and Henson, 2001).

Next, we introduce similar definitions for attenuant and resonance 2-cycles that are perturbations of 2-cycles. When a 2-cycle comes off of the 2-cycle of the unforced model, $\{\overline{x}, \overline{y}\}$, we use the following definition to compare the average of the 2-cycle with the average of $\{\overline{x}, \overline{y}\}$.

Definition 2. A 2-cycle of Model (2) is attenuant (resonant) if its average value is less (greater) than $\frac{\overline{x}+\overline{y}}{2}$.

When two 2-cycles come off of the 2-cycle of the unforced model, $\{\overline{x}, \overline{y}\}$, we use the following definition to compare the average of the two 2-cycles together with the average of $\{\overline{x}, \overline{y}\}$.

Definition 3. Let $\{\overline{x}_0, \overline{x}_1\}$ and $\{\overline{y}_0, \overline{y}_1\}$ denote two coexisting 2-cycles of Model (2) that come off of $\{\overline{x}, \overline{y}\}$. Together, $\{\overline{x}_0, \overline{x}_1\}$ and $\{\overline{y}_0, \overline{y}_1\}$, are attenuant (resonant) if their average value

$$\frac{\overline{x}_0 + \overline{y}_0 + \overline{x}_1 + \overline{y}_1}{4}$$

is less (greater) than $\frac{\overline{x}+\overline{y}}{2}$.

By these definitions, attenuant and resonant cycles refer to a decrease and an increase in average total population sizes, respectively.

3. 2-cycle population oscillations: 2-cycle bifurcation from unforced carrying capacity

Henson (1999) showed that small perturbations of a single parameter can generate population cycles of period 2. In this section, as in Kot and Schaffer (1984) and Rodriguez (1988), we illustrate that small 2-periodic perturbations of the carrying capacity and the demographic characteristic of populations governed by Model (1) produce 2-cycle populations, $\{x_0, x_1\}$ with x_0 and x_1 near k. This 2-cycle reduces to the carrying capacity in the absence of period-2 forcing in the parameters.

Theorem 4. *Suppose*

$$\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)} \neq 0$$

and

$$\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)} \neq -\frac{2}{k}.$$

Then for all sufficiently small $|\alpha|$ and $|\beta|$, Model (2) has a 2-cycle population

$$\{x_0 = x_0(\alpha, \beta), x_1 = x_1(\alpha, \beta)\},$$

where

$$\lim_{(\alpha,\beta)\to(0,0)} x_0(\alpha, \beta) = \lim_{(\alpha,\beta)\to(0,0)} x_1(\alpha, \beta) = k$$

and $x_0(\alpha, \beta), x_1(\alpha, \beta)$ are C^3 with respect to α and β. If the carrying capacity, k, is locally asymptotically stable (unstable), then the 2-cycle is locally asymptotically stable (unstable).

Proof: Let

$$F(\alpha, \beta, k, r, x) = f_{k(1-\alpha),r(1-\beta)} \circ f_{k(1+\alpha),r(1+\beta)}(x).$$

To prove this result, we look for fixed points of the composition map

$$F(\alpha, \beta, k, r, x) = xg(k(1+\alpha), r(1+\beta), x)\, g(k(1-\alpha), r(1-\beta), xg(k(1+\alpha), r(1+\beta), x)).$$

Note that $F(0, 0, k, r, k) = k$ and

$$\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,k)} = \left(1 + k \left.\frac{\partial g}{\partial x}\right|_{(k,r,k)}\right)^2.$$

Since $\frac{\partial g}{\partial x}|_{(k,r,k)} \neq 0$ and $\frac{\partial g}{\partial x}|_{(k,r,k)} \neq -\frac{2}{k}$, $\frac{\partial F}{\partial x}|_{(0,0,k,r,k)} \neq 1$. The Theorem follows from a direct application of the Implicit Function Theorem to F. □

The carrying capacity, k, is a hyperbolic fixed point of $f_{k,r}$ if $|\frac{df_{k,r}}{dx}(k)| \neq 1$. When k is a hyperbolic fixed point of $f_{k,r}$, then $\frac{\partial g}{\partial x}|_{(k,r,k)} \neq 0$, $\frac{\partial g}{\partial x}|_{(k,r,k)} \neq -\frac{2}{k}$ and the following result is immediate.

Corollary 5. *If the carrying capacity is a hyperbolic fixed point of Model (1), then for all sufficiently small $|\alpha|$ and $|\beta|$, Model (2) has a 2-cycle population*

$$\{x_0 = x_0(\alpha, \beta), x_1 = x_1(\alpha, \beta)\},$$

where

$$\lim_{(\alpha,\beta)\to(0,0)} x_0(\alpha, \beta) = \lim_{(\alpha,\beta)\to(0,0)} x_1(\alpha, \beta) = k$$

and $x_0(\alpha, \beta), x_1(\alpha, \beta)$ are C^3 with respect to α and β. If the carrying capacity, k, is locally asymptotically stable (unstable), then the 2-cycle is locally asymptotically stable (unstable).

By Corollary 5, Table 1 gives parameter regimes for the occurrence of a locally stable 2-cycle in six specific population models under small period two perturbations of the carrying capacity and the demographic characteristic of the species. Since these population models can have up to three coexisting 2-cycles (two stable and one unstable), these are not the only such parameter regimes.

4. Resonance versus attenuance: 2-cycle bifurcation from unforced carrying capacity

Small perturbations of a single parameter usually generate either attenuant or resonant cycles, but not both (Henson, 1999). We show that small perturbations of the carrying capacities and the demographic characteristics of the species (two parameters) generate both attenuant and resonant 2-cycles, depending on the relative strengths of the fluctuations. In this section, as in the previous section, we assume that the 2-cycle must, for small forcing, be close to the carrying capacity. For this 2-cycle, we develop a signature function, R_{d}, for determining whether the average total biomass is suppressed via attenuance or enhanced via resonance.

When the carrying capacity, k, is a hyperbolic fixed point of $f_{k,r}$, Corollary 5 guarantees that the 2-cycle solution of Model (2) can be expanded in terms of α

and β as follows:

$$x_0(\alpha,\beta) = k + x_{01}\alpha + x_{02}\beta + x_{011}\alpha^2 + x_{012}\alpha\beta + x_{022}\beta^2 + R_0(\alpha,\beta), \tag{3}$$

where $x_{01}, x_{02}, x_{011}, x_{012}, and x_{022}$ are the coefficients and $\lim_{(\alpha,\beta)\to(0,0)} \frac{R_0(\alpha,\beta)}{\alpha^2+\beta^2} = 0$. The expansion of the second point in the 2-cycle in terms of α and β is as follows:

$$x_1(\alpha,\beta) = k + x_{11}\alpha + x_{12}\beta + x_{111}\alpha^2 + x_{112}\alpha\beta + x_{122}\beta^2 + R_1(\alpha,\beta), \tag{4}$$

where $x_{11}, x_{12}, x_{111}, x_{112}, and x_{122}$ are the coefficients and $\lim_{(\alpha,\beta)\to(0,0)} \frac{R_1(\alpha,\beta)}{\alpha^2+\beta^2} = 0$.

We will use the following two auxiliary lemmas concerning the coefficients in Eqs. (3) and (4) to establish the following expression for the average of the 2-cycle:

$$\frac{x_0(\alpha,\beta)+x_1(\alpha,\beta)}{2} = k + \frac{(x_{011}+x_{111})}{2}\alpha^2 + \frac{(x_{012}+x_{112})}{2}\alpha\beta + \frac{R_0(\alpha,\beta)+R_1(\alpha,\beta)}{2}. \tag{5}$$

Lemma 6. *In Eqs. (3, 4),*

$$x_{02} = x_{12} = x_{022} = x_{122} = 0.$$

Proof: When $\alpha = 0$,

$$x_0(0,\beta) = k + x_{02}\beta + x_{022}\beta^2 + R_0(0,\beta)$$

and

$$x_1(0,\beta) = k + x_{12}\beta + x_{122}\beta^2 + R_1(0,\beta).$$

However, the fixed point of $f_{k,r(1\pm\beta)}$ is k. Thus,

$$f_{k,r(1-\beta)} \circ f_{k,r(1+\beta)}(k) = k,$$

and

$$x_0(0,\beta) = x_1(0,\beta) = k.$$

Therefore,

$$x_{02} = x_{12} = x_{022} = x_{122} = 0.$$

□

By this result, the coefficients of the relative strength β and β^2 in Eqs. (3) and (4) are zero. The next result establishes that the sum of the coefficients of the relative strength α in Equations (3) and (4) are zero.

Lemma 7. *In Eqs. (3, 4), if*

$$\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)} \neq 0,$$

then

$$x_{01} + x_{11} = 0.$$

Proof: Since

$$x_1(\alpha,\beta) = f_{k(1+\alpha),r(1+\beta)}(x_0(\alpha,\beta)) = x_0(\alpha,\beta)g(k(1+\alpha), r(1+\beta), x_0(\alpha,\beta)),$$
$$x_{11} = \left.\frac{\partial\,[x_0(\alpha,\beta)g(k(1+\alpha), r(1+\beta), x_0(\alpha,\beta))]}{\partial\alpha}\right|_{(\alpha,\beta,k,r,x)=(0,0,k,r,k)}.$$

Similarly,

$$x_0(\alpha,\beta) = f_{k(1-\alpha),r(1-\beta)}(x_1(\alpha,\beta)) = x_1(\alpha,\beta)g(k(1-\alpha), r(1-\beta), x_1(\alpha,\beta))$$

implies

$$x_{01} = \left.\frac{\partial\,[x_1(\alpha,\beta)g(k(1-\alpha), r(1-\beta), x_1(\alpha,\beta))]}{\partial\alpha}\right|_{(\alpha,\beta,k,r,x)=(0,0,k,r,k)}.$$

Therefore,

$$x_{11} = x_{01}\left(1 + k\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)}\right) + k^2\left.\frac{\partial g}{\partial k}\right|_{(k,r,k)}$$

and

$$x_{01} = x_{11}\left(1 + k\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)}\right) - k^2\left.\frac{\partial g}{\partial k}\right|_{(k,r,k)}.$$

Adding produces

$$(x_{01} + x_{11})\,k\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)} = 0.$$

Since $k \neq 0$ and $\left.\frac{\partial g}{\partial x}\right|_{(k,r,k)} \neq 0$,

$$x_{01} + x_{11} = 0.$$

□

Let

$$\mathcal{R}_{\mathrm{d}} = \begin{cases} \operatorname{sign}(w_1\alpha + w_2\beta) & \text{if } \alpha > 0 \\ 0 & \text{if } \alpha = 0 \\ -\operatorname{sign}(w_1\alpha + w_2\beta) & \text{if } \alpha < 0 \end{cases},$$

where $w_1 = \frac{(x_{011}+x_{111})}{2}$ and $w_2 = \frac{(x_{012}+x_{112})}{2}$. $\mathcal{R}_{\mathrm{d}}$ is the sign of a weighted sum of the relative strengths of the oscillations of the carrying capacity and the demographic characteristic of the species. A compact expression for $\mathcal{R}_\mathrm{d}$ is

$$\mathcal{R}_\mathrm{d} = \mathrm{sign}(\alpha(w_1\alpha + w_2\beta)).$$

In the following result, we show that $\mathcal{R}_\mathrm{d}$ determines when the 2-cycle is either attenuant or resonant.

Theorem 8. *If the carrying capacity is a hyperbolic fixed point of Model (1), then for all sufficiently small $|\alpha|$ and $|\beta|$, Model (2) has an attenuant (a resonant) 2-cycle if $\mathcal{R}_\mathrm{d}$ is negative (positive).*

Proof: Lemmas (6, 7) establish that the average of the 2-cycle predicted in Corollary 5 satisfies the equation

$$\begin{aligned}\frac{x_0(\alpha,\beta)+x_1(\alpha,\beta)}{2} &= k + \frac{(x_{011}+x_{111})}{2}\alpha^2 + \frac{(x_{012}+x_{112})}{2}\alpha\beta + \frac{R_0(\alpha,\beta)+R_1(\alpha,\beta)}{2}\\ &= k + \alpha\,(w_1\alpha + w_2\beta) + \frac{R_0(\alpha,\beta)+R_1(\alpha,\beta)}{2}.\end{aligned}$$

Since, $\lim_{(\alpha,\beta)\to(0,0)} \frac{R_0(\alpha,\beta)}{\alpha^2+\beta^2} = \lim_{(\alpha,\beta)\to(0,0)} \frac{R_1(\alpha,\beta)}{\alpha^2+\beta^2} = 0$, the sign of

$$\frac{x_0(\alpha,\beta)+x_1(\alpha,\beta)}{2} - k$$

is the same as the sign of $\alpha\,(w_1\alpha + w_2\beta)$ which is $\mathcal{R}_\mathrm{d}$, for all sufficiently small $|\alpha|$ and $|\beta|$ and $\mathcal{R}_\mathrm{d} \neq 0$. If $\frac{x_0(\alpha,\beta)+x_1(\alpha,\beta)}{2} - k > 0$, then the 2-cycle is resonant and if $\frac{x_0(\alpha,\beta)+x_1(\alpha,\beta)}{2} - k < 0$, then the 2-cycle is attenuant. □

When the demographic characteristic is fluctuating but the carrying capacity is constant ($\alpha = 0$ and $\beta \neq 0$), the 2-cycle degenerates into a fixed point at the carrying capacity. However, when the demographic characteristic is constant but the carrying capacity is fluctuating ($\alpha \neq 0$ and $\beta = 0$) Theorem 8 and the definition of $\mathcal{R}_\mathrm{d}$ give the following result.

Corollary 9. *If the carrying capacity is a hyperbolic fixed point of Model (1) and only the carrying capacity is fluctuating ($\beta = 0$), then for all sufficiently small $|\alpha|$,*

$$\mathcal{R}_\mathrm{d} = \mathrm{sign}(w_1)$$

and Model (2) has an attenuant (a resonant) 2-cycle if w_1 is negative (positive).

Population models with two periodically forced parameters are capable of experiencing both resonance and attenuance. We formalize this in the following result.

Corollary 10. *If the carrying capacity is a hyperbolic fixed point of Model (1), then for all sufficiently small $|\alpha|$ and $|\beta|$, Model (2) has an attenuant (a resonant)*

2-cycle if $w_2 > 0, \alpha > 0$ *and* $\beta < -\frac{w_1}{w_2}\alpha$ $(\beta > -\frac{w_1}{w_2}\alpha)$*. Also, Model (2) has an attenuant (a resonant) 2-cycle if* $w_2 < 0, \alpha > 0$ *and* $\beta > -\frac{w_1}{w_2}\alpha$ $(\beta < -\frac{w_1}{w_2}\alpha)$*. Consequently, if* $w_2 \neq 0$ *the model has both attenuant and resonant cycles.*

Proof: If $w_2 > 0, \alpha > 0$ and $\beta < -\frac{w_1}{w_2}\alpha$, then $w_2\beta < -w_1\alpha$, $w_1\alpha + w_2\beta < 0$, $\alpha(w_1\alpha + w_2\beta) < 0$ and $\mathcal{R}_\mathrm{d}$ is negative. Thus, Theorem 8gives that the 2-cycle is attenuant. Similar arguments establish the rest of the proof. □

In computing $\mathcal{R}_\mathrm{d}$, one usually needs to know the values of the weights w_1 and w_2. The formulas for these weights in terms of the carrying capacity, the demographic characteristic, the per capita growth rate, g, and its partial derivatives are given in the appendix.

5. $\mathcal{R}_\mathrm{d}$ for classical 2-periodic population models: 2-cycle bifurcation from unforced carrying capacity

In this section, we use our theorems to study the combined effects of fluctuating carry capacity and demographic characteristic on the average total biomass of the species that are governed by all the population models in Table 1. Specifically, we compute $\mathcal{R}_\mathrm{d}$ and use it to investigate parameter regimes of attenuance and resonance of the 2-cycle that comes off of the carrying capacity.

5.1. Model I

When both the carrying capacity and the demographic characteristic are 2-periodically forced, then the classic Ricker model becomes

$$x(t+1) = x(t)e^{r(1+\beta(-1)^t)\left(1-\frac{x(t)}{k(1+\alpha(-1)^t)}\right)}. \tag{6}$$

In Model I, $r > 0$ and $k > 0$. From Table 1, in constant environment, the carrying capacity, k, is asymptotically stable when $0 < r < 2$. If $0 < r < 2$, Corollary 5 predicts a stable 2-cycle in Model (6).

To determine the effects of periodicity on the 2-cycle, we use the formulas from the appendix to obtain that $\mathcal{R}_\mathrm{d} = \mathrm{sign}(\alpha(w_1\alpha + w_2\beta))$, where

$$w_1 = \frac{2k}{r-2},$$
$$w_2 = -\frac{2k}{r-2}.$$

Since $w_1 < 0$ $(w_1 > 0)$ when $r < 2$ $(r > 2)$, Corollary (9) predicts that when the demographic characteristic is constant, Model (6) has an attenuant (resonant) 2-cycle.

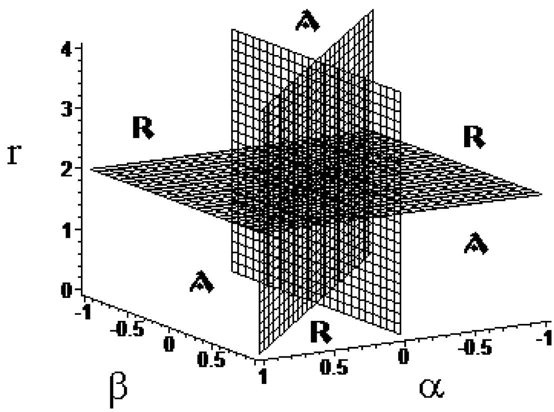

Fig. 1 Regions of attenuance and resonance in the α, β, r plane for the 2-periodic Ricker model.

If $0 < r < 2$ and $\alpha > 0$,

$$\mathcal{R}_\mathrm{d} = \mathrm{sign}(\frac{2k}{r-2}(\alpha-\beta)) = \mathrm{sign}(\beta-\alpha),$$

and the 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than the relative strength of the fluctuation of the carrying capacity.

If $0 < r < 2$ and $\alpha < 0$,

$$\mathcal{R}_\mathrm{d} = \mathrm{sign}(\alpha-\beta).$$

The regions of attenuance and resonance are determined by three equations in $\alpha, \beta, andr$. Figure 1 shows the graphs of these three equations

$$\alpha = 0, \alpha = \beta, r = 2,$$

and the regions of attenuance, denoted by **A**, and resonance, denoted by **R**.

5.2. Model II

When both the carrying capacity and the demographic characteristic are 2-periodically forced, then the classic Beverton–Holt model becomes

$$x(t+1) = x(t)\frac{k(1+\alpha(-1)^t)r(1+\beta(-1)^t)}{k(1+\alpha(-1)^t)+(r(1+\beta(-1)^t)-1)x(t)}. \tag{7}$$

In Model II, $r > 1$ and $k > 0$. From Table 1, in constant environment, the carrying capacity, k, is always asymptotically stable. Corollary 5) predicts a stable 2-cycle in Model (7).

To determine the effects of periodicity on the 2-cycle, we use the formulas from the appendix to obtain that $\mathcal{R}_d = \text{sign}(\alpha(w_1\alpha + w_2\beta))$, where

$$w_1 = \frac{-4kr}{(r+1)^2},$$
$$w_2 = \frac{2kr}{r^2-1}.$$

Since $w_1 < 0$, Corollary 9 predicts that when the demographic characteristic is constant, Model II has an attenuant 2-cycle. This is in agreement with the results of Cushing and Henson (2001), Elaydi and Sacker (2003, 2005, in press-a,b), Kocic (in press), and Kon (in press-a,b).

Since $r > 1$, if $\alpha > 0$,

$$\mathcal{R}_d = \text{sign}\left(\frac{-2}{r+1}\alpha + \frac{1}{r-1}\beta\right),$$

and the 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than $\frac{2(r-1)}{r+1}$ times the relative strength of the fluctuation of the carrying capacity.

If $\alpha < 0$,

$$\mathcal{R}_d = \text{sign}\left(\frac{2}{r+1}\alpha - \frac{1}{r-1}\beta\right).$$

The regions of attenuance and resonance are determined by two equations in $\alpha, \beta, andr$. Figure 2 shows the graphs of these two equations

$$\alpha = 0, \frac{2}{r+1}\alpha = \frac{1}{r-1}\beta,$$

and the regions of attenuance, denoted by **A**, and resonance, denoted by **R**.

5.3. Model III

When both the carrying capacity and the demographic characteristic are 2-periodically forced, then the Logistic model becomes

$$x(t+1) = x(t)\left(1 + r(1 + b(-1)^t)\left(1 - \frac{x(t)}{k(1 + a(-1)^t)}\right)\right). \tag{8}$$

In Model III, $r > 0$ and $k > 0$. From Table 1, in constant environment, the carrying capacity, k, is asymptotically stable when $0 < r < 2$. If $0 < r < 2$, Corollary 5 predicts a stable 2-cycle in Model III.

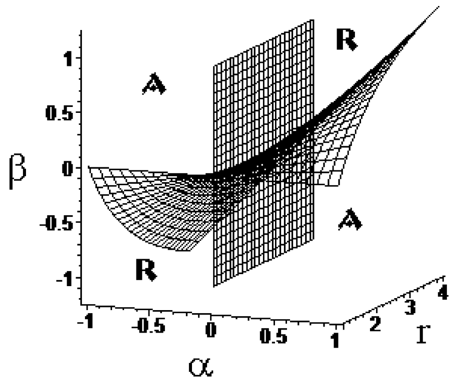

Fig. 2 Regions of attenuance and resonance in the α, β, r plane for the 2-periodic Beverton–Holt model.

To determine the effects of periodicity on the 2-cycle, we use the formulas from the appendix to obtain that $\mathcal{R}_\mathrm{d} = \mathrm{sign}(\alpha(w_1\alpha + w_2\beta))$, where

$$w_1 = \frac{-8k}{(r-2)^2},$$
$$w_2 = \frac{-4k}{r-2}.$$

Since $w_1 < 0$, Corollary 9 predicts that when the demographic characteristic is constant, Model (8) always has an attenuant 2-cycle.

If $0 < r < 2$ and $\alpha > 0$,

$$\mathcal{R}_\mathrm{d} = \mathrm{sign}\left(\frac{2}{r-2}\alpha + \beta\right),$$

and the 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than $\frac{2}{2-r}$ times the relative strength of the fluctuation of the carrying capacity.

If $0 < r < 2$ and $\alpha < 0$,

$$\mathcal{R}_\mathrm{d} = \mathrm{sign}\left(\frac{2}{2-r}\alpha - \beta\right).$$

The regions of attenuance and resonance are determined by three equations in $\alpha, \beta, andr$. Figure 3 shows the graphs of these three equations

$$\alpha = 0, \frac{2}{2-r}\alpha = \beta, r = 2,$$

and the regions of attenuance, denoted by **A**, and resonance, denoted by **R**. Since these three surfaces intersect in a line, there is actually no changing from

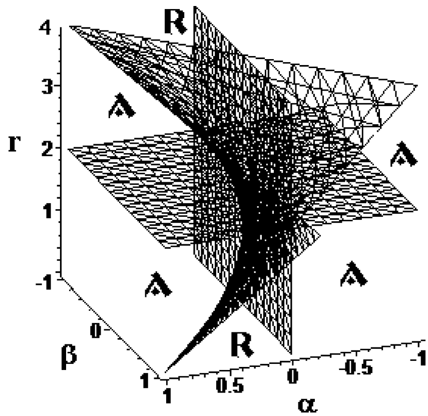

Fig. 3 Regions of attenuance ($\mathcal{A}$) and resonance ($\mathcal{R}$) in the α, β, r plane for the 2-periodic Logistic model.

attenuance to resonance or resonance to attenuance as we cross the $r = 2$ plane. From Figure 3, we see that it is much easier to have attenuance than resonance.

5.4. Model IV

When both the carrying capacity and the demographic characteristic are 2-periodically forced, then the model introduced by Hassell in 1974 becomes

$$x(t+1) = x(t)\frac{(1+k(1+\alpha(-1)^t))^{r(1+\beta(-1)^t)}}{(1+x(t))^{r(1+\beta(-1)^t)}}. \tag{9}$$

In Model IV, $r > 0$ and $k > 0$. From Table 1, in constant environment, the carrying capacity, k, is asymptotically stable when $rk < 2(1+k)$. If $rk < 2(1+k)$, Corollary 5 predicts a stable 2-cycle in Model (9).

To determine the effects of periodicity on the 2-cycle, we use the formulas from the appendix to obtain that $\mathcal{R}_\mathrm{d} = \mathrm{sign}(\alpha(w_1\alpha + w_2\beta))$, where

$$w_1 = \frac{2k^2(-1-k+kr)}{(-2-2k+kr)^2}$$

$$w_2 = \frac{-2k(1+k)}{-2-2k+kr}.$$

Figure 4 shows the regions where w_1 and w_2 are either positive or negative.

Since $w_1 < 0$ ($w_1 > 0$), when

$$-1-k+kr < 0\,(-1-k+kr > 0),$$

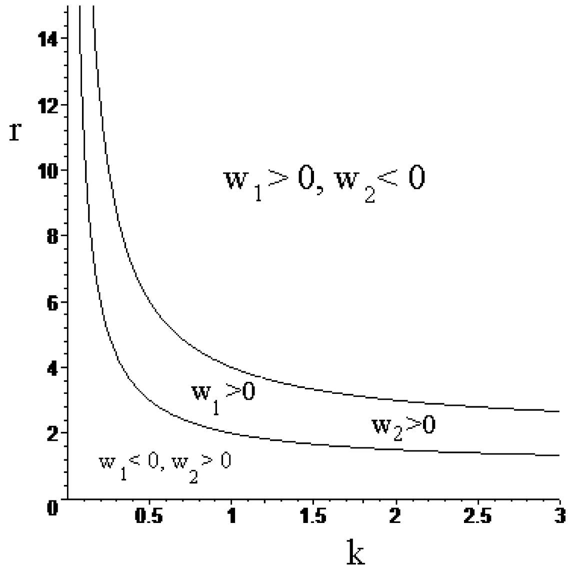

Fig. 4 Regions in the kr-plane where w_1 and w_2 are positive and negative for the 2-periodic Hassell model.

Corollary 9 predicts that when the demographic characteristic is constant, Model (9) has an attenuant (resonant) 2-cycle, when

$$-1 - k + kr < 0\ (-1 - k + kr > 0).$$

In particular, $-1 - k + kr < 0$ implies $rk < 2(1 + k)$, the condition for stability of the carrying capacity (see Table 1). The stable fixed point in constant environment of Model (9) can generate either a resonant or attenuant stable 2-cycle in a periodic environment. That is, in Model (9), a periodic environment is not always deleterious.

If $\alpha > 0$,

$$\mathcal{R}_d = \text{sign}\left(\frac{1}{-2 - 2k + kr}\left(\frac{k(-1 - k + kr)}{(-2 - 2k + kr)(1 + k)}\alpha - \beta\right)\right).$$

If, in addition, the carrying capacity is stable in constant environment, i.e.

$$rk < 2(1 + k),$$

then the 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than $\frac{k(-1-k+kr)}{(-2-2k+kr)(1+k)}$ times the relative strength of the fluctuation of the carrying capacity.

If $\alpha < 0$,

$$\mathcal{R}_d = \text{sign}\left(\frac{-1}{-2-2k+kr}\left(\frac{k(-1-k+kr)}{(-2-2k+kr)(1+k)}\alpha - \beta\right)\right).$$

5.5. Model V

When both the carrying capacity and the demographic characteristic are 2-periodically forced, then the model introduced by Smith in 1974 becomes

$$x(t+1) = x(t)\frac{(k(1+\alpha(-1)^t))^2 r(1+\beta(-1)^t)}{(k(1+\alpha(-1)^t))^2 + (r(1+\beta(-1)^t)-1)x(t)^2}. \tag{10}$$

In Model V, $r > 1$ and $k > 0$. From Table 1, in constant environment, the carrying capacity, k, is always asymptotically stable, and Corollary 5 predicts a stable 2-cycle in Model (10).

To determine the effects of periodicity on the 2-cycle, we use the formulas from the appendix to obtain that $\mathcal{R}_\text{d} = \text{sign}(\alpha(w_1\alpha + w_2\beta))$, where

$$w_1 = \frac{kr(r-4)}{2},$$
$$w_2 = \frac{kr}{r-1}.$$

Since $w_1 > 0$ ($w_1 < 0$) when $r < 4$ ($r > 4$), Corollary 9) predicts that when the demographic characteristic is constant, Model (10) can generate either resonant or attenuant 2-cycles as in Model (9).

Since $r > 1$, if $\alpha > 0$,

$$\mathcal{R}_\text{d} = \text{sign}\left(\frac{r-4}{2}\alpha + \frac{1}{r-1}\beta\right),$$

and the 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than $\frac{(1-r)(r-4)}{2}$ times the relative strength of the fluctuation of the carrying capacity.

If $\alpha < 0$,

$$\mathcal{R}_d = -\text{sign}\left(\frac{r-4}{2}\alpha + \frac{1}{r-1}\beta\right).$$

The regions of attenuance and resonance are determined by two equations in α, β, *andr*. Figure 5 shows the graphs of these two equations

$$\alpha = 0, \frac{r-4}{2}\alpha + \frac{1}{r-1}\beta = 0,$$

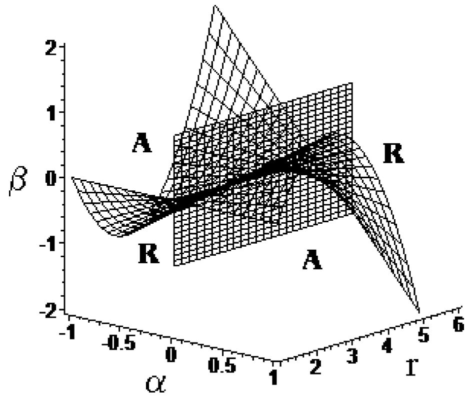

Fig. 5 Regions of attenuance and resonance in the α, β, r plane for the 2-periodic Smith Model V.

and the regions of attenuance, denoted by **A**, and resonance, denoted by **R**.

5.6. Model VI

When both the carrying capacity and the demographic characteristic are 2-periodically forced, then the model introduced by Smith in 1974 becomes

$$x(t+1) = x(t)\frac{(k(1+\alpha(-1)^t))^c\, r(1+\alpha(-1)^t)}{(k(1+\alpha(-1)^t))^c + (r(1+\alpha(-1)^t)-1)\,(x(t))^c}. \tag{11}$$

In Model VI, $r > 1, c > 0$, and $k > 0$. Our theory extends to models with more than two parameters, where the extra parameters do not fluctuate. From Table 1, in constant environment, the carrying capacity, k, is asymptotically stable when $c(r-1) < 2r$. If $c(r-1) < 2r$, Corollary 5 predicts a stable 2-cycle in Model (11).

To determine the effects of periodicity on the 2-cycle, we use the formulas from the appendix to obtain that $\mathcal{R}_{\rm d} = \text{sign}(\alpha(w_1\alpha + w_2\beta))$, where

$$w_1 = \frac{2kr(-r-2c+cr)}{(-2r-c+cr)^2}$$

$$w_2 = \frac{-2kr}{(-2r-c+cr)(r-1)}.$$

Figure 6 shows the regions where w_1 and w_2 are either positive or negative.

Since $w_1 < 0$ ($w_1 > 0$), when

$$-r-2c+cr < 0\,(-r-2c+cr > 0),$$

Corollary 9 predicts that when the demographic characteristic is constant, Model (11) has an attenuant (resonant) 2-cycle, when $-r-2c+cr < 0$ ($-r-2c+cr > 0$). If $0 < c < 1$ or $c > 3$, as in Model (7), the stable fixed point in constant

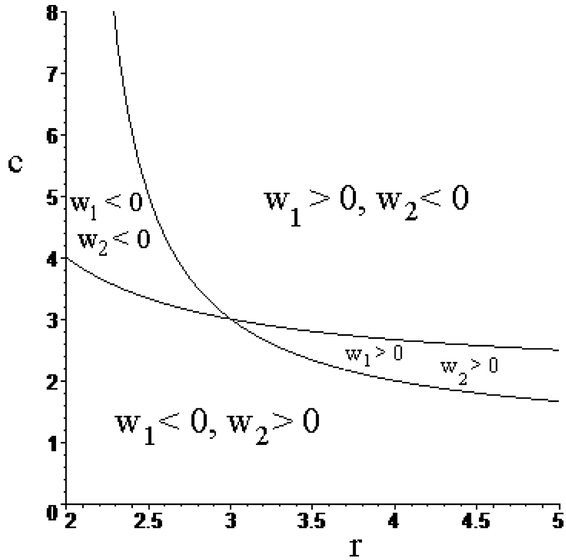

Fig. 6 Regions in the cr-plane where w_1 and w_2 are positive and negative for the 2-periodic Smith model.

environment of Model VI always generates an attenuant stable 2-cycle in a periodic environment. If $1 < c < 3$, as in Model (9), the stable fixed point in constant environment of Model VI can generate a resonant or an attenuant stable 2-cycle in a periodic environment. That is, in Model (11), a periodic environment is not always deleterious.

If $\alpha > 0$,

$$\mathcal{R}_d = \text{sign}\left(\frac{1}{-2r - c + cr}\left(\frac{-r - 2c + cr}{-2r - c + cr}\alpha - \frac{1}{r-1}\beta\right)\right).$$

If, in addition, the carrying capacity is stable in constant environment, i.e.

$$c(r-1) < 2r,$$

then the 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than $\frac{(-r-2c+cr)(r-1)}{-2r-c+cr}$ times the relative strength of the fluctuation of the carrying capacity.

If $\alpha < 0$,

$$\mathcal{R}_d = \text{sign}\left(\frac{-1}{-2r - c + cr}\left(\frac{-r - 2c + cr}{-2r - c + cr}\alpha - \beta\right)\right).$$

We list the $\mathcal{R}_d$ values of all six models in the following table:

A8

Table 2 $\mathcal{R}_d$ for multiparameter periodic population models $\mathcal{R}_d = \text{sign}(\alpha(w_1\alpha + w_2\beta))$.

Model number	w_1	w_2
6	$\frac{2k}{r-2}$	$-\frac{2k}{r-2}$
7	$\frac{-4kr}{(r+1)^2}$	$\frac{2kr}{r^2-1}$
8	$\frac{-8k}{(r-2)^2}$	$\frac{-4k}{r-2}$
9	$\frac{2k^2(-1-k+kr)}{(-2-2k+kr)^2}$	$\frac{-2k(1+k)}{-2-2k+kr}$
10	$\frac{kr(r-4)}{2}$	$\frac{kr}{r-1}$
11	$\frac{2kr(-r-2c+cr)}{(-2r-c+cr)^2}$	$\frac{-2kr}{(-2r-c+cr)(r-1)}$

6. 2-cycle population oscillations: 2-cycle bifurcation from unforced 2-cycle

In constant environments, simple (autonomous) unimodal population models such as the logistic and Ricker maps are capable of undergoing period-doubling bifurcations. In this section, we illustrate that small 2-periodic perturbations of a 2-cycle of Model (1), denoted by $\{\overline{x}, \overline{y}\}$, produce two 2-cycle populations, $\{\overline{x}_0, \overline{x}_1\}$ and $\{\overline{y}_0, \overline{y}_1\}$ with $\overline{x}_0, \overline{y}_1$ near $\overline{x}$ and $\overline{x}_1, \overline{y}_0$ near $\overline{y}$. These two 2-cycles reduce to the 2-cycle $\{\overline{x}, \overline{y}\}$ in the absence of period-2 forcing in the parameters.

Recall that in the absence of period-2 forcing our model reduces to

$$f_{k,r}(x) = xg(k, r, x).$$

Unlike the previous sections, we now assume throughout that $f_{k,r}(x)$ has a 2-cycle, $\{\overline{x}, \overline{y}\}$. Next, we proceed as in Theorem 2 and use the Implicit Function Theorem to show that, for small forcing, two coexisting 2-cycles come off of $\{\overline{x}, \overline{y}\}$. In the following result,

$$F(\alpha, \beta, k, r, x) = f_{k(1-\alpha),r(1-\beta)} \circ f_{k(1+\alpha),r(1+\beta)}(x).$$

Theorem 1. *Assume $f_{k,r}(x)$ has a hyperbolic 2-cycle, $\{\overline{x}, \overline{y}\}$. Then for all sufficiently small $|\alpha|$ and $|\beta|$, Model (2) has a pair of 2-cycle populations*

$$\{\overline{x}_0 = \overline{x}_0(\alpha, \beta), \overline{x}_1 = \overline{x}_1(\alpha, \beta)\}$$

and

$$\{\overline{y}_0 = \overline{y}_0(\alpha, \beta), \overline{y}_1 = \overline{y}_1(\alpha, \beta)\}$$

where

$$\lim_{(\alpha,\beta)\to(0,0)} \overline{x}_0(\alpha, \beta) = \overline{x}, \quad \lim_{(\alpha,\beta)\to(0,0)} \overline{x}_1(\alpha, \beta) = \overline{y},$$

$$\lim_{(\alpha,\beta)\to(0,0)} \overline{y}_1(\alpha, \beta) = \overline{x}, \quad \lim_{(\alpha,\beta)\to(0,0)} \overline{y}_0(\alpha, \beta) = \overline{y},$$

and $\overline{x}_0(\alpha,\beta), \overline{x}_1(\alpha,\beta)$, $\overline{y}_0(\alpha,\beta), \overline{y}_1(\alpha,\beta)$*are* C^3 *with respect to* α *and* β*. If the 2-cycle,* $\{\overline{x},\overline{y}\}$*, is locally asymptotically stable (unstable), then the two 2-cycles are locally asymptotically stable (unstable).*

Proof:

$$\begin{aligned} F(\alpha,\beta,k,r,x) &= f_{k(1-\alpha),r(1-\beta)}(f_{k(1+\alpha),r(1+\beta)}(x)) \\ &= xg(k(1+\alpha),r(1+\beta),x)g(k(1-\alpha),r(1-\beta), \\ &\quad xg(k(1+\alpha),r(1+\beta),x)). \end{aligned}$$

Consequently, $F(0,0,k,r,\overline{x})=\overline{x}$ and $F(0,0,k,r,\overline{y})=\overline{y}$. The 2-cycle, $\{\overline{x},\overline{y}\}$, is a hyperbolic fixed point of $f^2_{k,r}$ if

$$\left|\frac{\partial f^2_{k,r}}{\partial x}(\overline{x})\right| = \left|\frac{\partial f_{k,r}}{\partial x}(\overline{x})\cdot\frac{\partial f_{k,r}}{\partial x}(\overline{y})\right| \neq 1.$$

Hence,

$$\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{x})} = \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})}\cdot\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} = \left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{y})} \neq 1.$$

As in the proof of Theorem 4, we apply the Implicit Function Theorem at $(0,0,k,r,\overline{x})$ and $(0,0,k,r,\overline{y})$ to get

$$\begin{aligned} \overline{x}_0 &= \overline{x}_0(\alpha,\beta) \\ \overline{y}_0 &= \overline{y}_0(\alpha,\beta) \end{aligned}$$

as two 2-parameter families of fixed points of F.

That is, $\overline{x}_0(\alpha,\beta)$ and $\overline{y}_0(\alpha,\beta)$ each gives us a 2-cycle for the 2-periodic dynamical system

$$\{f_{k(1-\alpha),r(1-\beta)}(x),\ f_{k(1+\alpha),r(1+\beta)}(x)\}.$$

Let $\overline{x}_1(\alpha,\beta) = f_{k(1+\alpha),r(1+\beta)}(\overline{x}_0(\alpha,\beta))$ and $\overline{y}_1(\alpha,\beta) = f_{k(1+\alpha),r(1+\beta)}(\overline{y}_0(\alpha,\beta))$. Note that

$$\overline{x}_0(\alpha,\beta) = f_{k(1-\alpha),r(1-\beta)}(\overline{x}_1(\alpha,\beta))$$

and

$$\overline{y}_0(\alpha,\beta) = f_{k(1-\alpha),r(1-\beta)}(\overline{y}_1(\alpha,\beta)).$$

□

7. Resonance versus attenuance: 2-cycle bifurcation from unforced 2-cycle

In Sect. 4, we developed a signature function, $\mathcal{R}_{\mathrm{d}}$, for determining whether the average total biomass is suppressed via attenuance or enhanced via resonance under the assumption that a 2-cycle must, for small forcing, be close to the carrying capacity. In this section, we obtain a signature function, $\mathcal{R}_{\mathrm{d}}$, under the assumption that a 2-cycle must, for small forcing, be close to the 2-cycle of Model (1).

Recall that when the 2-cycle $\{\overline{x}, \overline{y}\}$ is hyperbolic, Theorem 11 guarantees the four 2-parameter families,

$$\overline{x}_0(\alpha,\beta), \overline{x}_1(\alpha,\beta), \overline{y}_0(\alpha,\beta) \ \textit{and} \ \overline{y}_1(\alpha,\beta),$$

where $\overline{x}_1(\alpha,\beta) = f_{k(1+\alpha),r(1+\beta)}(\overline{x}_0(\alpha,\beta))$ and $\overline{y}_1(\alpha,\beta) = f_{k(1+\alpha),r(1+\beta)}(\overline{y}_0(\alpha,\beta))$. Note that

$$\overline{x}_0(\alpha,\beta) = f_{k(1-\alpha),r(1-\beta)}(\overline{x}_1(\alpha,\beta))$$

and

$$\overline{y}_0(\alpha,\beta) = f_{k(1-\alpha),r(1-\beta)}(\overline{y}_1(\alpha,\beta)).$$

Let the linear expansion of these four 2-parameter families about $(\alpha,\beta) = (0,0)$ be

$$\overline{x}_0(\alpha,\beta) = \overline{x} + x_{01}\alpha + x_{02}\beta,$$
$$\overline{x}_1(\alpha,\beta) = \overline{y} + x_{11}\alpha + x_{12}\beta,$$
$$\overline{y}_0(\alpha,\beta) = \overline{y} + y_{01}\alpha + y_{02}\beta,$$
$$\overline{y}_1(\alpha,\beta) = \overline{x} + y_{11}\alpha + y_{12}\beta.$$

We now find formulas for the coefficients x_{0i}, x_{1i}, y_{0i}, and y_{1i} for each $i \in \{1,2\}$.

$$x_{01} = -\frac{\left.\frac{\partial F}{\partial \alpha}\right|_{(0,0,k,r,\overline{x})}}{\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{x})} - 1} = -\frac{-k\left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{y})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left(k\left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{x})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1},$$

$$x_{02} = -\frac{\left.\frac{\partial F}{\partial \beta}\right|_{(0,0,k,r,\overline{x})}}{\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{x})} - 1} = -\frac{-r\left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{y})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left(r\left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{x})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1},$$

$$y_{01} = -\frac{\left.\frac{\partial F}{\partial \alpha}\right|_{(0,0,k,r,\overline{y})}}{\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{y})} - 1} = -\frac{-k\left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{x})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} \cdot \left(k\left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{y})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1},$$

$$y_{02} = -\frac{\left.\frac{\partial F}{\partial \beta}\right|_{(0,0,k,r,\overline{y})}}{\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{y})} - 1} = -\frac{-r\left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{x})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} \cdot \left(r\left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{y})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1}.$$

To compute the other four coefficients, we let $\overline{F}(\alpha, \beta, k, r, x) = F(-\alpha, -\beta, k, r, x)$ and observe that

$$\overline{F}(\alpha, \beta, k, r, \overline{x}_1(\alpha, \beta)) = \overline{x}_1(\alpha, \beta)$$

and

$$\overline{F}(\alpha, \beta, k, r, \overline{y}_1(\alpha, \beta)) = \overline{y}_1(\alpha, \beta).$$

Then

$$x_{11} = -\frac{\left.\frac{\partial \overline{F}}{\partial \alpha}\right|_{(0,0,k,r,\overline{y})}}{\left.\frac{\partial \overline{F}}{\partial x}\right|_{(0,0,k,r,\overline{y})} - 1} = -\frac{k \left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{x})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} \cdot \left(-k \left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{y})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1},$$

$$x_{12} = -\frac{\left.\frac{\partial \overline{F}}{\partial \beta}\right|_{(0,0,k,r,\overline{y})}}{\left.\frac{\partial \overline{F}}{\partial x}\right|_{(0,0,k,r,\overline{y})} - 1} = -\frac{r \left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{x})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} \cdot \left(-r \left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{y})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1},$$

$$y_{11} = -\frac{\left.\frac{\partial \overline{F}}{\partial \alpha}\right|_{(0,0,k,r,\overline{x})}}{\left.\frac{\partial \overline{F}}{\partial x}\right|_{(0,0,k,r,\overline{x})} - 1} = -\frac{k \left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{y})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left(-k \left.\frac{\partial f_{k,r}}{\partial k}\right|_{(\overline{x})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1},$$

$$y_{12} = -\frac{\left.\frac{\partial \overline{F}}{\partial \beta}\right|_{(0,0,k,r,\overline{x})}}{\left.\frac{\partial \overline{F}}{\partial x}\right|_{(0,0,k,r,\overline{x})} - 1} = -\frac{r \left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{y})} + \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left(-r \left.\frac{\partial f_{k,r}}{\partial r}\right|_{(\overline{x})}\right)}{\left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{y})} \cdot \left.\frac{\partial f_{k,r}}{\partial x}\right|_{(\overline{x})} - 1}.$$

Let

$$\mathcal{R}_{\mathrm{d}}(\overline{x}) = w_{1x}\alpha + w_{2x}\beta$$

and

$$\mathcal{R}_{\mathrm{d}}(\overline{y}) = w_{1y}\alpha + w_{2y}\beta,$$

where

$$w_{ix} = x_{0i} + x_{1i}$$

and

$$w_{iy} = y_{0i} + y_{1i}$$

for each $i \in \{1, 2\}$. As in Sect. 4, when the two 2-cycles come off of the 2-cycle in the unforced model, the signature function $\mathcal{R}_{\mathrm{d}}$ is a weighted sum of the relative strengths of the oscillations of the carrying capacity and the demographic characteristic of the species.

Lemma 12. *Assume* $f_{k,r}(x)$ *has a 2-cycle,* $\{\overline{x}, \overline{y}\}$. *Suppose*

$$\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{x})} \neq 1$$

and

$$\left.\frac{\partial F}{\partial x}\right|_{(0,0,k,r,\overline{y})} \neq 1.$$

Then for all sufficiently small $|\alpha|$ *and* $|\beta|$, *Model (2) has a pair of 2-cycle populations*

$$\{\overline{x}_0 = \overline{x}_0(\alpha, \beta), \overline{x}_1 = \overline{x}_1(\alpha, \beta)\}$$

and

$$\{\overline{y}_0 = \overline{y}_0(\alpha, \beta), \overline{y}_1 = \overline{y}_1(\alpha, \beta)\},$$

where

$$\mathcal{R}_{\mathrm{d}}(\overline{x}) + \mathcal{R}_{\mathrm{d}}(\overline{y}) = 0.$$

The proof of Lemma 12 is in the appendix.

The next result shows that, under the assumption that a 2-cycle must, for small forcing, be close to the 2-cycle of Model (1), the pair of two 2-cycles, $\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\}$ *and* $\{\overline{y}_0(\alpha, \beta), \overline{y}_1(\alpha, \beta)\}$, are respectively either resonant and attenuant or vice versa; for most values of the relative strengths of the oscillations of the carrying capacity and the demographic characteristic of the species.

Theorem 13. *Assume* $f_{k,r}(x)$ *has a hyperbolic 2-cycle,* $\{\overline{x}, \overline{y}\}$.*If*

$$x_{01} + x_{11} \neq 0$$

and

$$x_{02} + x_{12} \neq 0,$$

then for each fixed ratio of (α, β), *except when*

$$\mathcal{R}_d(\overline{x}) = (x_{01} + x_{11})\alpha + (x_{02} + x_{12})\beta = 0,$$

there is a neighborhood of $(0, 0)$ *such that on one side*

$$\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\} \text{ and } \{\overline{y}_0(\alpha, \beta), \overline{y}_1(\alpha, \beta)\}$$

are attenuant and resonant, respectively. On the other side,

$$\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\} \text{ and } \{\overline{y}_0(\alpha, \beta), \overline{y}_1(\alpha, \beta)\}$$

are also resonant and attenuant, respectively.

The proof of Theorem 13 is in the appendix.

Another question is to compare the average of all four points on the two 2-cycles with the average of $\overline{x}$ and $\overline{y}$. Since $\mathcal{R}_{\rm d}(\overline{x}) + \mathcal{R}_{\rm d}(\overline{y}) = 0$, the answer to this question comes from a second order form in (α, β). Let

$$\mathcal{R}_{\rm d}(\overline{x}, \overline{y}) = w_{11}\alpha^2 + w_{12}\alpha\beta + w_{22}\beta^2,$$

where

$$\begin{aligned} w_{11} &= x_{011} + x_{111} + y_{011} + y_{111} \\ w_{12} &= x_{012} + x_{112} + y_{012} + y_{112} \\ w_{22} &= x_{022} + x_{122} + y_{022} + y_{122}. \end{aligned}$$

For a fixed ratio of (α, β), the sign of $\mathcal{R}_{\rm d}(\overline{x}, \overline{y})$ does not change. Thus, if $\mathcal{R}_{\rm d}(\overline{x}, \overline{y}) > 0$ for some (α, β), the four points will give resonance for some small values of (α, β). If $\mathcal{R}_{\rm d}(\overline{x}, \overline{y})$ is positive and negative for different choices of (α, β), then the four points will give resonance for certain small values and give attenuance for other small values.

8. $\mathcal{R}_{\rm d}$ for classical 2-periodic population models: 2-cycle bifurcation from unforced 2-cycle

The Ricker and Logistic maps are capable of supporting 2-cycles (Models I and III from Table 1). In this section, we use our theorems to study the combined effects of fluctuating carry capacity and demographic characteristic on the average total biomass of the species when 2-cycles come off of the 2-cycle in the unforced Logistic or Ricker model. Specifically, we compute $\mathcal{R}_{\rm d}$ and use it to illustrate parameter regimes of attenuance and resonance of the 2-cycles that come off of the 2-cycle of the unforced models.

8.1. Model I

When $r = 2$, the classic Ricker model undergoes period doubling bifurcation. The carrying capacity becomes unstable and a stable 2-cycle is formed. In fact, the Ricker model has a 2-cycle whenever $r > 2$.

Example 14. In the Ricker model, let $r = 2.1$ and $k = 1$.

With the above choice of parameters, the Ricker model has an attracting 2-cycle at

$$\{0.6292942674, 1.370705732\}.$$

Calculating derivatives at these points yields

$$x_{01} + x_{11} = -8.518460 + 7.777049 = -0.741\,41 \neq 0$$

and

$$x_{02} + x_{12} = -1.086682 + 1.828093 = 0.741\,41 \neq 0.$$

By Theorem 13, with the advent of 2-periodic forcing in Example 14, we usually obtain two 2-cycles and one of these 2-cycles is attenuant while the other one is resonant.

Next, we compare the average of the two 2-cycles together in the forced system with the unforced single 2-cycle in Example 14. Calculating second partials, we obtain that

$$w_{11} = -98.54947,$$
$$w_{12} = 154.47951,$$
$$w_{22} = 9.13211,$$
$$\text{and } \mathcal{R}_d(\bar{x}, \bar{y}) = -98.54947\alpha^2 + 154.47951\alpha\beta + 9.13211\beta^2.$$

Thus, when β is small compared to α, then the two 2-cycles are attenuant. However, when $\beta > \alpha$ the two 2-cycles are resonant.

For example when

$$\alpha = 0.001 \quad \text{and} \quad \beta = 0$$

the two 2-cycles are

$$\{1.362508521, 0.6382137735 \quad \textit{and} \quad \{0.6211238366, 1.378117170\}.$$

The first one, $\{1.362508521, 0.6382137735\}$, is a resonant 2-cycle and the second one, $\{0.6211238366, 1.378117170\}$, is an attenuant 2-cycle. The average of all the four points is 0.9999908. Thus, $\mathcal{R}_d(\bar{x}, \bar{y}) < 0$ and together the two 2-cycles are attenuant.

For a second example, we reset the parameters α and β so that

$$\alpha = 0.001 \quad \text{and} \quad \beta = 0.002.$$

In this case, the two 2-cycles are

$$\{1.381722313, 0.6190423680\} \quad \textit{and} \quad \{0.6404986537, 1.358785059\}.$$

The first one, $\{1.381722313, 0.6190423680\}$, is a resonant 2-cycle and the second one, $\{0.6404986537, 1.358785059\}$, is an attenuant 2-cycle. The average of all the four points is 1.0000121. Thus, $\mathcal{R}_d(\bar{x}, \bar{y}) > 0$ and together the two 2-cycles are resonant.

8.2. Model III

As in the Ricker model, when $r = 2$, the Logistic model undergoes period doubling bifurcation. Similarly, its carrying capacity becomes unstable and a stable 2-cycle is formed. The formulas for these period 2 points are

$$\overline{x} = \left(1 + \frac{r}{2} + \frac{\sqrt{r^2 - 4}}{2}\right)\frac{k}{r},$$
$$\overline{y} = \left(1 + \frac{r}{2} - \frac{\sqrt{r^2 - 4}}{2}\right)\frac{k}{r}.$$

The Logistic model is more mathematically tractable and is the only population model in Table 1 for which there are simple closed form formulas for the 2-cycle. These formulas make it possible to determine the resonance and attenuance of the two 2-cycles that form with the advent of period-two forcing.

The coefficients for the linear terms in the expansion for $\overline{x}_0$ and $\overline{x}_1$ are

$$x_{01} = -\frac{\left(2 + r + \sqrt{-4 + r^2}\right)^2 k\left(2\sqrt{-4 + r^2} - r^2 + r\sqrt{-4 + r^2}\right)}{8r(4 - r^2)},$$
$$x_{02} = \frac{\left(2 + r + \sqrt{-4 + r^2}\right) k\left(\sqrt{-4 + r^2} - r + 2\right)\sqrt{-4 + r^2}}{4r(4 - r^2)},$$
$$x_{11} = -\frac{\left(-2 - r + \sqrt{-4 + r^2}\right)^2 k\left(2\sqrt{-4 + r^2} + r^2 + r\sqrt{-4 + r^2}\right)}{8r(4 - r^2)},$$
$$x_{12} = \frac{\left(-2 - r + \sqrt{-4 + r^2}\right) k\left(\sqrt{-4 + r^2} + r - 2\right)\sqrt{-4 + r^2}}{4r(4 - r^2)}.$$

Combining these give

$$w_{1x} = x_{01} + x_{11} = \frac{\sqrt{r^2 - 4})k}{r - 2},$$
$$w_{2x} = x_{02} + x_{10} = 0.$$

Since $w_{2x} = 0$, the resonance of the new 2-cycle depends only on α. Since $r > 2$, $w_{1x} > 0$. When $\alpha > 0$, this 2-cycle is resonant and the other one is attenuant.

To determine the resonance or attenuance of the two 2-cycles together, we need to calculate the second order terms in the expansion of $\overline{x}_0, \overline{x}_1, \overline{y}_0$, and $\overline{y}_1$. These are found by taking second partials of the equations

$$F(\alpha, \beta, k, r, \overline{x}_0(\alpha, \beta)) = \overline{x}_0(\alpha, \beta)$$
$$F(\alpha, \beta, k, r, \overline{y}_0(\alpha, \beta)) = \overline{y}_0(\alpha, \beta)$$

$$\overline{F}(\alpha, \beta, k, r, \overline{x}_1(\alpha, \beta)) = \overline{x}_1(\alpha, \beta)$$
$$\overline{F}(\alpha, \beta, k, r, \overline{y}_1(\alpha, \beta)) = \overline{y}_1(\alpha, \beta),$$

and evaluating at $\alpha = 0, \beta = 0$. We also use that the first order terms have already been calculated. These equations are then solved for the appropriate second order term. The 12 second-order terms are:

$$x_{011} = \frac{2k(r^3 - r^2\sqrt{-4+r^2} - 2r\sqrt{-4+r^2} - 4r + 2\sqrt{-4+r^2})}{r(r^4 - 4r^3 + 16r - 16)},$$
$$x_{012} = -\frac{(r^2 - 2\sqrt{-4+r^2})k}{(-2+r)r\sqrt{-4+r^2}},$$
$$x_{022} = \frac{k(r^2 - 4 - \sqrt{-4+r^2}))}{r(-4+r^2)},$$
$$x_{111} = \frac{2k(r^3 + r^2\sqrt{-4+r^2} + 2r\sqrt{-4+r^2} - 4r - 2\sqrt{-4+r^2})}{r(r^4 - 4r^3 + 16r - 16)},$$
$$x_{112} = \frac{(r^2 + 2\sqrt{-4+r^2})k}{(-2+r)r\sqrt{-4+r^2}},$$
$$x_{122} = \frac{k(r^2 - 4 + \sqrt{-4+r^2}))}{r(-4+r^2)},$$
$$y_{011} = \frac{2k(r^3 + r^2\sqrt{-4+r^2} + 2r\sqrt{-4+r^2} - 4r - 2\sqrt{-4+r^2})}{r(r^4 - 4r^3 + 16r - 16)},$$
$$y_{012} = \frac{(r^2 + 2\sqrt{-4+r^2})k}{(-2+r)r\sqrt{-4+r^2}},$$
$$y_{022} = \frac{k(r^2 - 4 + \sqrt{-4+r^2}))}{r(-4+r^2)}$$
$$y_{111} = \frac{2k(r^3 - r^2\sqrt{-4+r^2} - 2r\sqrt{-4+r^2} - 4r + 2\sqrt{-4+r^2})}{r(r^4 - 4r^3 + 16r - 16)}$$
$$y_{112} = -\frac{(r^2 - 2\sqrt{-4+r^2})k}{(-2+r)r\sqrt{-4+r^2}},$$
$$y_{122} = \frac{k(r^2 - 4 - \sqrt{-4+r^2}))}{r(-4+r^2)}.$$

Using the four points from the two 2-cycles gives

$$\mathcal{R}_{\mathrm{d}}(\overline{x}, \overline{y}) = w_{11}\alpha^2 + w_{12}\alpha\beta + w_{22}\beta^2,$$

where

$$w_{11} = x_{011} + x_{111} + y_{011} + y_{111},$$
$$w_{12} = x_{012} + x_{112} + y_{012} + y_{112},$$
$$w_{22} = x_{022} + x_{122} + y_{022} + y_{122}.$$

Using the derived second-order terms gives

$$w_{11} = \frac{8k}{r^2 - 4r + 4},$$
$$w_{12} = \frac{8k}{r(-2 + r)},$$
$$w_{22} = \frac{4k}{r}.$$

Substituting these expressions into $\mathcal{R}_d$ gives

$$\begin{aligned}
\mathcal{R}_d(\overline{x}, \overline{y}) &= \frac{8k}{r^2 - 4r + 4}\alpha^2 + \frac{8k}{r(-2+r)}\alpha\beta + \frac{4k}{r}\beta^2 \\
&= \frac{8k}{(r-2)^2}\alpha^2 + \frac{8k}{r(-2+r)}\alpha\beta + \frac{4k}{r}\beta^2 \\
&= 4k\left(\frac{2}{(r-2)^2}\alpha^2 + \frac{2}{r(-2+r)}\alpha\beta + \frac{r}{r^2}\beta^2\right) \\
&\geq 4k\left(\frac{1}{(r-2)^2}\alpha^2 + \frac{2}{r(-2+r)}\alpha\beta + \frac{1}{r^2}\beta^2\right) \\
&= 4k\left(\frac{1}{r-2}\alpha + \frac{1}{r}\beta\right)^2 \geq 0.
\end{aligned}$$

Thus, together the two 2-cycles in the Logistic model are always resonant.

Next, we consider specific examples of the Logistic model.

Example 15. In the Logistic model, Model III of Table 1, let

$$r = 3 \text{ and } k = 1.$$

In this example, the 2-cycle of the unforced Model III is

$$\left\{\frac{5+\sqrt{5}}{6}, \frac{5-\sqrt{5}}{6}\right\}.$$

In addition, let

$$\alpha = 0.001 \quad and \quad \beta = 0.001.$$

Then, the 2-periodically forced model has three 2-cycles. The 2-cycle off of the unstable fixed point is

$$\{1.002994090, 0.9969939095\},$$

which is attenuant since its coordinates add up to less than 2. The two 2-cycles coming off of the 2-cycle of the unforced Logistic model are

$$\{0.4590456012, 1.205390950\} \quad and \quad \{1.206626976, 0.4622818075\}.$$

The coordinates of the first 2-cycle add up to $1.664436551 < \frac{5}{3}$, while that of the second 2-cycle add up to $1.668908784 > \frac{5}{3}$. That is, the first one is an attenuant 2-cycle and the second one is resonant. Adding all four of the points of the two 2-cycles together gives $3.333345334 > \frac{10}{3}$. As predicted, together the two 2-cycles are resonant.

9. Conclusion

There have been many experimental and theoretical studies on the effects of fluctuating environments on populations (Moran, 1950; Nicholson, 1954; Ricker, 1954; Beverton and Holt, 1957; Utida, 1957; Pennycuick et al., 1968; Smith, 1968; Hassell, 1974; May, 1974a,b; Smith, 1974; Hassell et al., 1976; May and Oster, 1976; May, 1977; Coleman, 1978; Fisher et al., 1979; Jillson, 1980; Rosenblat, 1980; Nisbet and Gurney, 1982; Nobile et al., 1982; Coleman and Frauenthal, 1983; Rosenkranz, 1983; Kot and Schaffer, 1984; Cull, 1986, 1988; Rodriguez, 1988; Yodzis, 1989; Li, 1992; Kocic and Ladas, 1993; Elaydi, 1994; Begon et al., 1996; Henson and Cushing, 1997; Costantino et al., 1998; Henson, 1999, 2000; Henson et al., 1999; Elaydi, 2000; Cushing and Henson, 2001; Selgrade and Roberds, 2001; Elaydi and Yakubu, 2002; Cull, 2003; Elaydi and Sacker, 2003, 2005, in press-a,b; Yakubu, 2005; Kocic, in press; Kon, in press-a,b). In constant environments, many classical, discrete-time single-species, population models have at least the two parameters, carrying capacity and demographic characteristic of the species (Moran, 1950; Nicholson, 1954; Ricker, 1954; Beverton and Holt, 1957; Pennycuick et al., 1968; Smith, 1968; Hassell, 1974; May, 1974a,b; Smith, 1974; Hassell et al., 1976; May and Oster, 1976; May, 1977; Nisbet and Gurney, 1982; Rosenkranz, 1983; Cull, 1986; Cull, 1988, 2003; Yodzis, 1989; Begon et al., 1996; Elaydi, 2000; Cushing and Henson, 2001; Franke and Yakubu, 2005a,b,c). The studies predict that populations are either enhanced or suppressed by periodic environments. In most theoretical studies, with only a few exceptions (see Kot and Schaffer, 1984; Rodriguez, 1988), only one parameter is periodically forced. It is known that unimodal maps under period-2 forcing in two model parameters routinely have up to three coexisting 2-cycles (Kot and Schaffer, 1984). Our results on ecological models with 2-periodically forced two model parameters support these predictions. We prove that small 2-periodic fluctuations of both the carrying capacity and the demographic characteristic of the species induce 2-cyclic oscillations of the populations. Furthermore, our results predict both attenuance and resonance in population models with two parameters that are 2-periodically forced. We introduce a signature function, $\mathcal{R}_{\mathrm{d}}$, for determining the response of discretely reproducing populations to periodic fluctuations of both their carrying capacity and demographic characteristic. $\mathcal{R}_{\mathrm{d}}$ is the sign of a weighted sum of the relative strengths of the oscillations of the carrying capacity and the demographic characteristic of the species. The periodic environments are deleterious for the population when $\mathcal{R}_{\mathrm{d}}$ is negative. However, the environments are favorable to the population when $\mathcal{R}_{\mathrm{d}}$ is positive. Our results predict that a change in the relative strengths of the environmental and demographic fluctuations can shift the system from attenuance to resonance and vice versa.

We compute $\mathcal{R}_{\mathrm{d}}$ for six periodically forced classical ecological models, and use $\mathcal{R}_{\mathrm{d}}$ to determine regions in parameter space that are either favorable or detrimental to the population. Next, we discuss three of the six models to illustrate the important points, where the periodic carrying capacity first decreases and then increases back to its initial value (relative strength, $\alpha > 0$), and in constant environments each model has a stable carrying capacity.

For the Ricker model, with the advent of periodicity, the stable 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than the relative strength of the fluctuation of the carrying capacity.

In 2-periodic environments, the stable 2-cycle of the classic Beverton–Holt model is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species is stronger (weaker) than about two times the relative strength of the fluctuation of the carrying capacity.

The classic Maynard Smith model, Model V, has a stable carrying capacity. In 2-periodic environments, its stable 2-cycle is resonant (attenuant) when the relative strength of the fluctuation of the demographic characteristic of the species, r, is stronger (weaker) than $\frac{(1-r)(r-4)}{2}$ times the relative strength of the fluctuation of the carrying capacity.

Furthermore, we prove that small 2-periodic perturbations of a 2-cycle of the unforced system produce two (coexisting) 2-cycle populations. We compute $\mathcal{R}_{\mathrm{d}}$ for the coexisting 2-cycles. Typically, if the unforced 2-cycle is unstable (stable) we get two unstable (stable) 2-cycles. In the Ricker model, we use examples to illustrate attenuant and resonant 2-cycles. However, in the Logistic model, together the two (coexisting) 2-cycles are always resonant.

Response of populations to periodic environments is a complex function of the period of the environments, the carrying capacities, the demographic characteristics, and the type and nature of the fluctuations. Our examples have highlighted some of these relationships via the signature function $\mathcal{R}_{\mathrm{d}}$ and the model parameters. Typically, our examples seem to indicate that an amplitude of oscillation of demographic characteristics greater than that in carrying capacity is needed to produce a resonant 2-cycle. Further investigations on these and their biological implications are welcome.

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Appendix

In this appendix, we obtain formulas for w_1, w_2 and provide proofs for Lemma 12 and Theorem 13.

First, we obtain formulas for $w_1 = \frac{x_{011}+x_{111}}{2}$ and $w_2 = \frac{x_{012}+x_{112}}{2}$ in terms of r, k, g, and $g's$ partial derivatives.

Using the Implicit Function Theorem on

$$F(\alpha,\beta,k,r,x) = xg(k(1+\alpha), r(1+\beta), x)\, g(k(1-\alpha), r(1-\beta), \\ xg(k(1+\alpha), r(1+\beta), x)\,)\,.$$

as in the proof of Theorem 4, we obtain the first derivative of $x_0(\alpha,\beta)$ at $(0,0)$ to be

$$x_{01} = -\frac{k^2\frac{\partial g}{\partial k}}{2+k\frac{\partial g}{\partial x}}.$$

Since

$$x_1(\alpha,\beta) = f_{k(1+\alpha),r(1+\beta)}(x_0(\alpha,\beta)) = x_0(\alpha,\beta)g(k(1+\alpha), r(1+\beta), x_0(\alpha,\beta)),$$

$$2x_{111} = \left.\frac{\partial^2\left[x_0(\alpha,\beta)g(k(1+\alpha), r(1+\beta), x_0(\alpha,\beta))\right]}{\partial\alpha^2}\right|_{(\alpha,\beta,k,r,x)=(0,0,k,r,k)}.$$

Similarly,

$$x_0(\alpha,\beta) = f_{k(1-\alpha),r(1-\beta)}(x_1(\alpha,\beta)) = x_1(\alpha,\beta)g(k(1-\alpha), r(1-\beta), x_1(\alpha,\beta))$$

implies

$$2x_{011} = \left.\frac{\partial^2\left[x_1(\alpha,\beta)g(k(1-\alpha), r(1-\beta), x_1(\alpha,\beta))\right]}{\partial\alpha^2}\right|_{(\alpha,\beta,k,r,x)=(0,0,k,r,k)}.$$

Therefore,

$$2\,(x_{111}+x_{011}) = 2\left(1+k\frac{\partial g}{\partial x}\right)(x_{111}+x_{011}) + \left(2k\frac{\partial^2 g}{\partial x^2}+4\frac{\partial g}{\partial x}\right)x_{01}^2 \\ + \left(4k\frac{\partial g}{\partial k}+4k^2\frac{\partial^2 g}{\partial x\partial k}\right)x_{01} + 2k^3\frac{\partial^2 g}{\partial k^2},$$

where all partial derivatives are evaluated at (k, r, k). Thus,

$$w_1 = \frac{\left(k\frac{\partial^2 g}{\partial x^2} + 2\frac{\partial g}{\partial x}\right) x_{01}^2 + \left(2k\frac{\partial g}{\partial k} + 2k^2\frac{\partial^2 g}{\partial x \partial k}\right) x_{01} + k^3\frac{\partial^2 g}{\partial k^2}}{-2k\frac{\partial g}{\partial x}}.$$

Similarly,

$$w_2 = -\frac{\left(r\frac{\partial g}{\partial r} + kr\frac{\partial^2 g}{\partial x \partial r}\right) x_{01} + k^2 r\frac{\partial^2 g}{\partial k \partial r}}{k\frac{\partial g}{\partial x}}.$$

Now substitute in $x_{01} = -\frac{k^2\frac{\partial g}{\partial k}}{2+k\frac{\partial g}{\partial x}}$ we obtain

$$w_1 = \frac{\left(k\frac{\partial^2 g}{\partial x^2} + 2\frac{\partial g}{\partial x}\right)\left(\frac{k^2\frac{\partial g}{\partial k}}{2+k\frac{\partial g}{\partial x}}\right)^2 + \left(2k\frac{\partial g}{\partial k} + 2k^2\frac{\partial^2 g}{\partial x \partial k}\right)\left(-\frac{k^2\frac{\partial g}{\partial k}}{2+k\frac{\partial g}{\partial x}}\right) + k^3\frac{\partial^2 g}{\partial k^2}}{-2k\frac{\partial g}{\partial x}}$$

and

$$w_2 = -\frac{\left(r\frac{\partial g}{\partial r} + kr\frac{\partial^2 g}{\partial x \partial r}\right)\left(-\frac{k^2\frac{\partial g}{\partial k}}{2+k\frac{\partial g}{\partial x}}\right) + k^2 r\frac{\partial^2 g}{\partial k \partial r}}{k\frac{\partial g}{\partial x}},$$

where all of the derivatives are evaluated at (k, r, k).

Proof of Lemma 12. *By Theorem (11), Model (2) has a pair of 2-cycle populations*

$$\{\overline{x}_0 = \overline{x}_0(\alpha, \beta), \overline{x}_1 = \overline{x}_1(\alpha, \beta)\}$$

and

$$\{\overline{y}_0 = \overline{y}_0(\alpha, \beta), \overline{y}_1 = \overline{y}_1(\alpha, \beta)\},$$

for all sufficiently small $|\alpha|$ *and* $|\beta|$.

Next, we show that $R_{\mathrm{d}}(\overline{x}) + R_{\mathrm{d}}(\overline{y}) = 0$.

$$x_{01}+x_{11}+y_{01}+y_{11}=$$

$$-\frac{-k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{y})} + \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{y})} * \left(k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{x})}\right)}{\left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{y})} * \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{x})} - 1} + -\frac{k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{x})} + \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{x})} * \left(-k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{y})}\right)}{\left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{y})} * \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{x})} - 1} +$$

$$-\frac{-k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{x})} + \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{x})} * \left(k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{y})}\right)}{\left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{y})} * \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{x})} - 1} + -\frac{k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{y})} + \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{y})} * \left(-k\left.\frac{\partial f}{\partial k}\right|_{(k,r,\overline{x})}\right)}{\left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{y})} * \left.\frac{\partial f}{\partial x}\right|_{(k,r,\overline{x})} - 1} = 0.$$

Similarly,

$$x_{02} + x_{12} + y_{02} + y_{12} = 0.$$

This completes the proof.

Proof of Theorem 13. *To investigate the resonance or attenuance of* $\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\}$ *we need to look at*

$$\overline{x}_0(\alpha, \beta) + \overline{x}_1(\alpha, \beta) - (\overline{x} + \overline{y}) = \mathcal{R}_d(\overline{x}) + \text{ higher order terms}.$$

Approaching the origin from one side along a fixed ratio of (α, β) *guarantees that the sign of* $R_\mathrm{d}(\overline{x})$ *does not change and that it eventually dominates the higher order terms. The sign of* $R_\mathrm{d}(\overline{x})$ *changes as we move to the other side of the origin. Thus if* $R_\mathrm{d}(\overline{x}) > 0$ *on one side of the origin,* $\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\}$ *is resonant on this side and attenuant on the other side. By the last lemma,* $R_\mathrm{d}(\overline{x}) = -R_\mathrm{d}(\overline{y})$ *and hence* $\{\overline{y}_0(\alpha, \beta), \overline{y}_1(\alpha, \beta)\}$ *will eventually be attenuant on the side where* $\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\}$ *is resonant and will eventually be resonant on the side where* $\{\overline{x}_0(\alpha, \beta), \overline{x}_1(\alpha, \beta)\}$ *is attenuant. This completes the proof.*

References

Begon, M., Harper, J.L., Townsend, C.R., 1996. Ecology: Individuals, populations and communities. Blackwell Science, Oxford.

Beverton, R.J.H., Holt, S.J., 1957. On the dynamics of exploited fish populations, H.M. Stationery Off., London. Fish. Invest. 2, 19.

Coleman, B.D., 1978. On the growth of populations with narrow spread in reproductive age. I. General theory and examples. J. Math. Biol. 6, 1–19.

Coleman, C.S., Frauenthal, J.C., 1983. Satiable egg eating predators, Math. Biosci. 63, 99–119.

Costantino, R.F., Cushing, J.M., Dennis, B., Desharnais, R. A., 1998. Resonant population cycles in temporarily fluctuating habitats. Bull. Math. Biol. 60, 247–273.

Cull, P., 1986. Local and global stability for population models. Biol. Cybern. 54, 141–149.

Cull, P., 1988. Stability of discrete one-dimensional population models. Bull. Math. Biol. 50(1), 67–75.

Cull, P., 2003. Stability in one-dimensional models. Sci. Math. Jpn. 58, 349–357.

Cushing, J.M., Henson, S.M., 2001. Global dynamics of some periodically forced, monotone difference equations. J. Diff. Equ. Appl. 7, 859–872.

Elaydi, S.N., 1994. Periodicity and stability of linear Volterra difference equations. J. Math. Anal. Appl. 181, 483-492.

Elaydi, S.N., 2000. Discrete Chaos. Chapman and Hall/CRC, Boca Raton, FL.

Elaydi, S.N., Sacker, R.J., 2003. Global stability of periodic orbits of nonautonomous difference equations. In: Population Biology and Cushing–Henson Conjectures. Proceedings of ICDEA8, Brno, in press). A3

Elaydi, S.N., Sacker, R.J., 2005. Global stability of periodic orbits of nonautonomous difference equations and population biology. J. Diff. Equ. 208(1), 258–273.

Elaydi, S.N., Sacker, R.J., in press-a. Nonautonomous Beverton–Holt equations and the Cushing–Henson conjectures. J. Diff. Equ. Appl. A4

Elaydi, S.N., Sacker, R.J., in press-b. Periodic difference equations, populations biology and the Cushing-Henson conjectures, preprint).

Elaydi, S.N., Yakubu, A.-A., 2002. Global stability of cycles: Lotka–Volterra competition model with stocking. J. Diff. Equ. Appl. 8(6), 537–549.

Fisher, M.E., Goh, B.S., Vincent, T.L., 1979. Some stability conditions for discrete-time single species models. Bull. Math. Biol. 41, 861–875.
Franke, J.E., Selgrade, J.F., 2003. Attractor for periodic dynamical systems. J. Math. Anal. Appl. 286, 64–79.
Franke, J.E., Yakubu, A.-A., 2005a. Periodic dynamical systems in unidirectional metapopulation models. J. Diff. Equ. Appl. 11(7), 687–700.
Franke, J.E., Yakubu, A.-A. 2005b. Multiple attractors via cusp bifurcation in periodically varying environments. J. Diff. Equ. Appl. 11(4–5), 365–377.
Franke, J.E., Yakubu, A.-A. 2005c. Population models with periodic recruitment functions and survival rates. J. Diff. Equ. Appl. 11(14), 1169–1184.
Hassell, M.P., 1974. Density dependence in single species populations. J. Anim. Ecol. 44, 283-296.
Hassell, M.P., Lawton, J.H., May, R.M., 1976. Patterns of dynamical behavior in single species populations. J. Anim. Ecol. 45, 471–486.
Henson, S.M., 1999. The effect of periodicity in maps. J. Diff. Equ. Appl. 5, 31–56.
Henson, S.M., 2000. Multiple attractors and resonance in periodically forced population models. Phys. D 140, 33–49.
Henson, S.M., Costantino, R.F., Cushing, J.M., Dennis, B., Desharnais, R.A., 1999. Multiple attractors, saddles, and population dynamics in periodic habitats. Bull. Math. Biol. 61, 1121–1149.
Henson, S.M., Cushing, J.M., 1997. The effect of periodic habitat fluctuations on a nonlinear insect population model. J. Math. Biol. 36, 201–226.
Jillson, D., 1980. Insect populations respond to fluctuating environments. Nature 288, 699–700.
Kocic, V.L., in press. A note on nonautonomous Beverton–Holt model. J. Diff. Equ. Appl. **A5**
Kocic, V.L., Ladas, G., 1993. Global behavior of nonlinear difference equations of higher order with applications. In: Mathematics and its Applications, Vol. 256. Kluwer Academic, Dordrecht, The Netherlands.
Kon, R., in press-a. A note on attenuant cycles of population models with periodic carrying capacity. J. Diff. Equ. Appl. **A6**
Kon, R., in press-b. Attenuant cycles of population models with periodic carrying capacity. J. Diff. Equ. Appl.
Kot, M., Schaffer, W.M., 1984. The effects of seasonality on discrete models of population growth. Theor. Popul. Biol. 26, 340–360.
Li, J., 1992. Periodic solutions of population models in a periodically fluctuating environment. Math. Biosci. 110, 17–25.
May, R.M., 1974a. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton, NJ.
May, R.M., 1974b. Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. Science 186, 645–647.
May, R.M., 1977. Simple mathematical models with very complicated dynamics. Nature 261, 459–469.
May, R.M., Oster, G.F., 1976. Bifurcations and dynamic complexity in simple ecological models. Am. Nat. 110, 573–579.
Moran, P.A.P., 1950. Some remarks on animal population dynamics. Biometrics 6, 250–258.
Nicholson, A.J., 1954. Compensatory reactions of populations to stresses, and their evolutionary significance. Aust. J. Zool. 2, 1–65.
Nisbet, R.M., Gurney, W.S.C., 1982. Modelling Fluctuating Populations, Wiley, New York.
Nobile, A., Ricciardi, L.M., Sacerdote, L., 1982. On Gompertz growth model and related difference equations. Biol. Cybern. 42, 221–229.
Pennycuick, C.J., Compton, R.M., Beckingham, L., 1968. A computer model for simulation the growth of a population, or of two interacting populations. J. Theor. Biol. 18, 316–329.
Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11, 559–623.
Rodriguez, D.J., 1988. Models of growth with density regulation in more than one life stage. Theor. Popul. Biol. 34, 93–117.
Rosenblat, S., 1980. Population models in a periodically fluctuating environment. J. Math. Biol. 9, 23–36.

Rosenkranz, G., 1983. On global stability of discrete population models. Math. Biosci. 64, 227–231.

Selgrade, J.F., Roberds, H.D., 2001. On the structure of attractors for discrete, periodically forced systems with applications to population models. Physica D 158, 69–82.

Smith, J.M., 1968. Mathematical ideas in biology. Cambridge University Press, Cambridge,England.

Smith, J.M., 1974. Models in Ecology. Cambridge University Press, Cambridge, UK.

Utida, S., 1957. Population fluctuation,an experimental and theoretical approach. Cold Spring Harbor Symp. Quant. Biol. 22, 139–151.

Yakubu, A.-A. 2005. Periodically forced nonlinear difference equations with delay. In: Allen, L., Aulbach, B., Elaydi, S., Sacker, R. (Eds.), Difference Equations and Discrete Dynamical Systems, Proceedings of the 9th International Conference, University of Southern California,
A7 California.

Yodzis, P., 1989. Introduction to Theoretical Ecology. Harper and Row, New York.

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